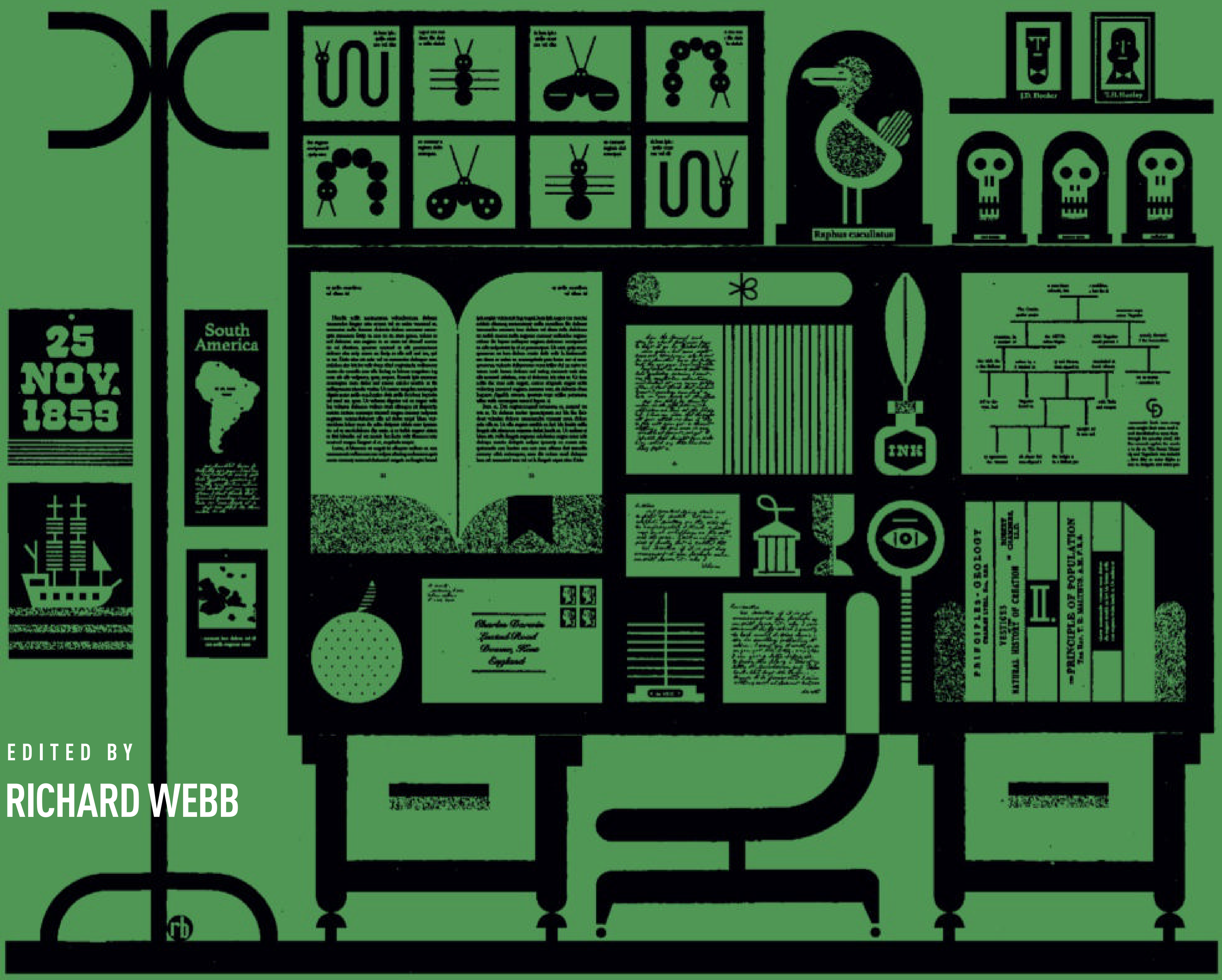
New Scientist

ESSENTIAL GUIDE №6

THE ORIGINS OF EVOLUTION
WHAT DARWIN DISCOVERED
GENETICS AND DNA
EVOLUTION MYTHS
AND MISCONCEPTIONS
THE FUTURE OF EVOLUTION
AND MORE

EVOLUTION

DARWIN'S THEORY OF NATURAL SELECTION AND WHAT IT MEANS FOR LIFE



EDITED BY
RICHARD WEBB

NEW SCIENTIST ESSENTIAL GUIDE
EVOLUTION

"THERE is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."

There can be no better words to introduce this latest *New Scientist Essential Guide* than those with which Charles Darwin closed his magisterial work of 1859, *On the Origin of Species*. The theory of evolution by natural selection introduced by Darwin in that book has few equals in the history of human intellectual achievement. It is an idea in its kernel so simple, yet in its scope so grand and its detail so complex, that we are still getting to grips with all its implications.

I hope you enjoy learning more about the nature of Darwin's ideas, how they arose and how our understanding of them has evolved and continues to evolve, in this *Essential Guide* – as indeed I did in putting it together. Do visit shop.newscientist.com to obtain more issues in the series; feedback is, as ever, welcome at essentialguides@newscientist.com.
Richard Webb

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HOW EVOLUTION BEGAN

Charles Darwin didn't invent the idea of evolution. But his groundbreaking ideas of how species adapt and change in response to their environment revolutionised our ideas of how life's astounding diversity arose – and aroused controversy from the start.

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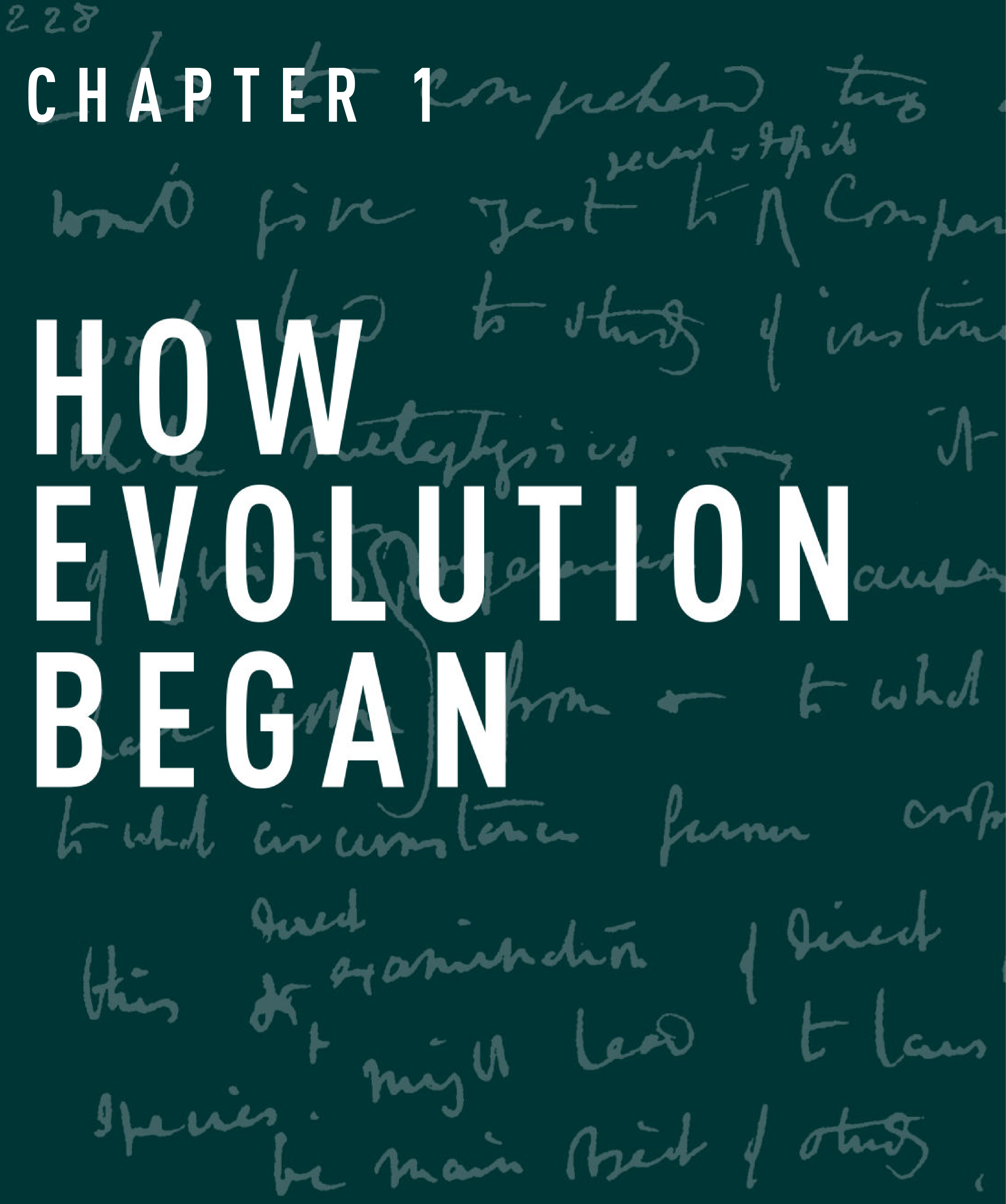

CHAPTER 1

HOW EVOLUTION BEGAN

Two centuries ago, answers as to what produced the astounding diversity of life forms around us didn't go much beyond the idea that they were all unchanging works of God.

Charles Darwin didn't invent the idea of evolution. But his groundbreaking theory of evolution by natural selection revolutionised our ideas of how life's astounding diversity arose, and gave us the framework with which we understand the natural world today. John van Wyhe takes up the story.

ON THE ORIGIN OF EVOLUTION

EVOLUTION is the most revolutionary concept in the history of science. Nothing else has more radically changed our understanding of the natural world and ourselves.

The work of Charles Darwin showed, irrefutably, that humans are just another animal occupying a small branch on a vast tree of life. No divine spark is needed to explain our existence and traits.

But how exactly did Darwin devise his theory of evolution? What ideas did he build on? Where does the naturalist Alfred Russel Wallace, who proposed a similar theory, fit in? And how shocking was the idea to the Christian society of the time?

The story of the uncovering of this great revelation has been retold countless times since the publication of Darwin's *On the Origin of Species* in 1859. In the process, the assumptions and guesses of one generation became accepted as fact by the next – with some spawning widespread myths. Perhaps the most fundamental of these is that thinkers had been striving for centuries to solve the mystery of the origin of species. They hadn't, and indeed they couldn't have – just as ancient Greek philosophers could not have been searching for dark matter.

Darwin's and Wallace's theory of evolution maintains that new species are descended from earlier ones. This long-term process happens because all ›

PROFILE
JOHN VAN WYHE

John van Wyhe is a historian of science at the National University of Singapore and the founder and director of *Darwin Online*, a searchable repository of all Charles Darwin's writings, available at darwin-online.org.uk

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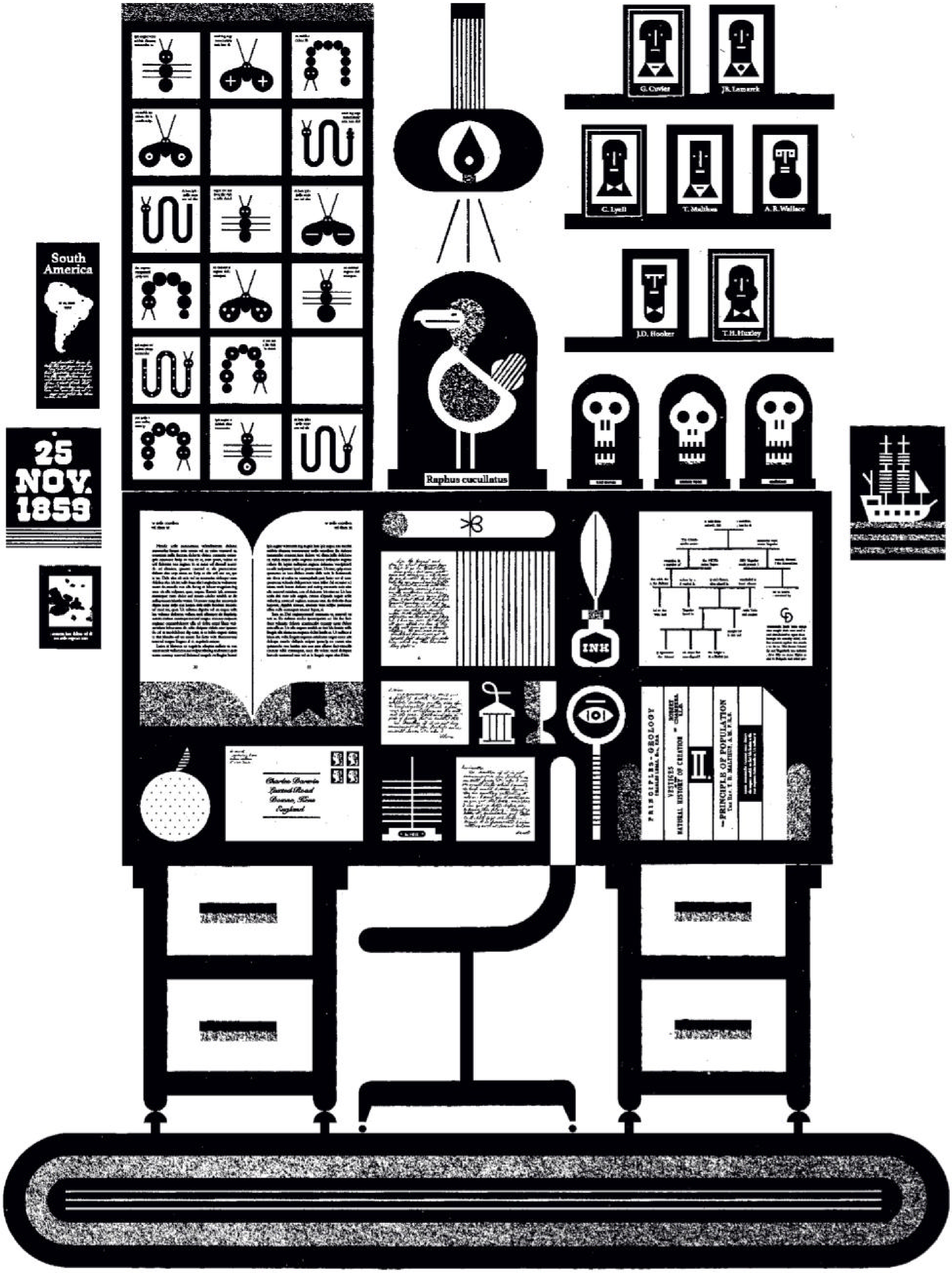
RIGHT: RAYMOND BIESINGER


South America
25 NOV. 1859
G. Cuvier
J.B. Lamarck
C. Lyell
T. Malthus
A.R. Wallace
J.D. Hooker
T.H. Huxley
Raphus cucullatus
INK
Charles Darwin
Luxted Road
Downe, Kent
England
PRINCIPLES OF GEOLOGY
VESTIGES OF THE NATURAL HISTORY OF CREATION
ROBERT CHAMBERS
II.
PRINCIPLE OF POPULATION
The Rev. T. R. MALTHUS, A.M. F.R.S.

“It’s hard to appreciate now how radical the idea of species going extinct was”

organisms vary. The tiny variations are naturally “selected” by virtue of whether or not they help an organism to survive the brutal struggle for existence in nature. Many are born, but few survive; fortuitous variations are preferentially passed on. This process of endless filtering works to adapt organisms to their environment.

Traditionally, people in Christian Europe had believed that the world was about 6000 years old. This view was guided by interpolations from the Bible, which itself gave no date for creation. Gradually such beliefs were modified by Christian thinkers based on new information about Earth, gleaned from the growth of mining and the development of geology. By the early 19th century it was widely understood that Earth could not be a few thousand years old, but must be inconceivably ancient.

Earth was also found to have changed over time. Close study of rocks and fossils revealed a complex history of different ages. One layer of the geological record might show lush tropical vegetation populated with reptiles unlike any alive today. In the rock layers just above, yet another terrestrial world might have existed with different animals and plants. To explain this, in 1812 the great French anatomist Georges Cuvier put forward the idea that each age had been abruptly ended by some great catastrophe.

Another puzzle was the discovery in Europe and the Americas of gigantic fossilised animals. Where could creatures such as mammoths be living today? Perhaps their kind had died out? This couldn’t be true, according to traditional belief, since God would not allow any of his created species to perish.

Cuvier’s detailed research in anatomy established, once and for all, that creatures such as the mammoth were not the same as anything alive today, and were extinct. For us, extinction is such a mundane fact that we cannot appreciate how radical the concept was initially. However, it soon became almost universally accepted in the scientific community, with one important exception: the French naturalist Jean-Baptiste Lamarck.

For Lamarck, these unfamiliar fossil forms had not gone extinct. Instead they had changed, evolving into something else – although his view of this process was different to that later proposed by Darwin (see “Evolution before Darwin”, right). The mammoth, for example, could have evolved into the elephant.

As the influential Cuvier did with so many rivals, he used his reputation to demolish Lamarck. The result was that for the first few decades of the 19th century, not only Lamarck’s theory but any theory of evolution was considered unscientific and absurd. Although Lamarck won a few converts, many more accepted Cuvier’s view that a succession of eras of life had come and gone.

But where did the new species that emerged after these extinctions come from? The geologist Charles Lyell argued in his *Principles of Geology*, published in the early 1830s, that slow processes had changed Earth over time. Lyell’s picture was one of perpetual change. As an environment gradually transformed, the species that lived in it would become unsuited to it and die out, because there was a limit to how much they could change to adapt. Just how new species arose was left vague.

Lyell's work was of great interest to Charles Darwin, a young Cambridge graduate who was appointed to join the surveying voyage of HMS Beagle as a naturalist in 1831 (contrary to popular accounts, he was not invited along to be the captain's social companion, nor was the ship's surgeon the official naturalist). During this five-year voyage, Darwin matured into one of the most experienced scientists of his generation. He worked primarily as a geologist but also collected a wide range of living things, from finches to fungi.

The expedition first visited South America, then surveyed the waters around the Galapagos Islands. Only in the middle of the 20th century did Darwin's visit there come to be portrayed as a pivotal moment in his life. He never described it as such. And as charming as it sounds, there is no truth to the story that Darwin noticed the beaks of the finches were adapted to different diets and that this provoked his evolutionary theorising. There was no Galapagos eureka moment.

After the return of HMS Beagle in 1836, Darwin set to work describing his mountain of specimens. He also began asking himself deep questions about nature, life and religion. Gradually, he gave up his belief in Christianity. "It is not supported by evidence," he concluded. Nevertheless, as far as we know, he never lost a belief in a supernatural creator behind nature.

Several types of evidence led Darwin to accept that species must evolve. On his voyage down the South American continent, he observed that related species gradually replaced one another. The species living in the Galapagos also puzzled him. Many of these were unique to the islands, yet most were strikingly similar to South American species. But the Galapagos,

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EVOLUTION BEFORE DARWIN

Lamarckism is mentioned in biology textbooks as shorthand for a pre-Darwinian theory of evolution in which species were thought to evolve via the inheritance of characteristics acquired during an organism's lifetime. According to this, the giraffe got its long neck by intentionally stretching to reach the top of trees. This slightly stretched neck was then passed on to offspring, and so on.

But this version of Lamarckism is a terrible caricature. The biologist Jean-Baptiste Lamarck did not originate this idea – which many naturalists, including Darwin, continued to accept –and this was not the core of his theory. Instead, Lamarck's central idea was that there is a tendency for life to progress up the scale of perfection according to a "complexifying force". New species originated continuously via spontaneous generation (the appearance of life from inorganic matter) and could adapt to local circumstances through the inheritance of acquired characteristics.

a collection of marine volcanoes, had never been connected to South America and their climate was totally different.

According to Lyell's view, species were somehow created to suit new environments. So why were the Galapagos species so obviously related to South American ones instead of just being rocky island species? Darwin's explanation was that their ancestors must have come from South America and changed over time.

In 1838, Darwin read Thomas Malthus's 1798 *An Essay on the Principle of Population*, which argued that continued population growth would lead to famine and starvation. Darwin was struck by the implications of checks to population growth. This led him to focus on what allowed some individuals rather than others to survive and pass on their characteristics.

He hypothesised that every organism varied in many small ways, and any of these variations that helped or hindered would make a difference to which survived. He eventually called this filtering process "natural selection" by analogy with the process in which farmers changed domesticated plants and animals by selecting desirable individuals to breed from. In so doing, they emphasised some traits and reduced others.

→
Turn to chapter 2 for more on how evolution works

It would take Darwin more than 20 years to publish these ideas. In recent decades it has become widely believed that Darwin kept his evolutionary theorising a secret and delayed its publication because he was afraid of the reaction. A large body of literature emerged proposing reasons for this: for example, that he was put off by the fierce reception to the 1844 evolutionary potboiler *Vestiges of the Natural History of Creation*, or that he was afraid of offending his religious wife. Yet there is not a shred of evidence for either suggestion.

In fact, Darwin told his family, friends and colleagues about his theory and his plans to publish it. He felt he had years of research to conduct before he would be ready and, like his other major works, the species theory took longer than he originally imagined. By early 1858, he had drafted many chapters and was about a year or two away from publishing his "big book", which would have spanned several volumes.

Then, on 18 June, something surprising happened. An essay arrived in the mail from Alfred Russel Wallace, outlining a theory almost identical to Darwin's own.

Wallace was a brilliant collector who had worked in south-eastern Asia since 1854. There are perhaps even more myths about him than Darwin. Wallace is often portrayed as the lower-class underdog to the genteel, moneyed Darwin. But Wallace was not working class, and neither was he forced to leave school early because of his family's finances. He was not deprived of his proper share of credit or made the victim of skulduggery by Darwin or his cronies, as is often claimed today. The underdog version of Wallace's story emerged only after the 1950s.

Wallace had long been privately convinced that species must evolve. But he was certainly not, as many modern commentators put it, searching for a mechanism for how evolution works. As he collected thousands of tropical insects and birds, his theoretical views gradually matured.

WHO WAS CHARLES DARWIN?

For someone who devised a revolutionary idea, Charles Darwin lived a remarkably quiet life. In 1842, Darwin and his wife Emma moved from London to rural Kent in southern England. They already had two children then, and would go on to have eight more.

Darwin had very regular habits. He rose early and went for a walk. After breakfast he worked in his study until 9.30 am, his most productive time of the day, then read his letters lying on the sofa before returning to work.

At midday he would go for another walk accompanied by his dog, stopping at his greenhouse to inspect his botanical experiments. Then he would proceed to the sand walk, a gravel path around a strip of woodland. While strolling on this "thinking path", Darwin would ruminate on his unsolved scientific problems.

After luncheon he read the newspaper and wrote letters. His network of correspondents provided information from all corners of the globe.

The Darwins were not very strict parents and the children were apt to run wild. Their mild-mannered father worked patiently to a background of playful screams and little footsteps stampeding past his study door.

After dinner Darwin played backgammon with his wife. They were very competitive. He once wrote, "Now the tally with my wife in backgammon stands thus: she, poor creature, has won only 2490 games, whilst I have won, hurrah, hurrah, 2795 games!"

Despite poor health, Darwin continued to publish a string of innovative and seminal works until his final book on earthworms in 1881. It was an instant bestseller. He died the following year, aged 73.

But science had one last claim on him. Rather than a quiet interment in the local churchyard, which he called "the sweetest place on Earth", Darwin was given a state funeral in London's Westminster Abbey.

FINEART/ALAMY STOCK PHOTO

In February 1858, on the tiny spice island of Ternate, Wallace lay sweating from fever when he thought of a means whereby species could become naturally adapted to a changing world. It was a filtering process of life and death that was very similar to Darwin's natural selection. When he recovered, Wallace wrote an essay, "On the tendency of varieties to depart indefinitely from the original type", aimed primarily at Lyell's anti-evolutionary arguments. Shortly after, Wallace received an encouraging letter from Darwin stating that Wallace's hero, Lyell, admired Wallace's work. This led Wallace to send the essay to Darwin with the request that it be forwarded to Lyell.

It has been claimed that Darwin might have lied about when he received the essay, leading to accusations that Darwin could have plagiarised Wallace. In fact, Darwin received the essay exactly when he said he did.

Darwin was struck by the resemblance between Wallace's views and his own. The same day, Darwin sent the essay on to Lyell, bemoaning that he ought to send it for publication ahead of his own work. For someone who was ever the Victorian country gentleman (see "Who was Charles Darwin?", left), it seemed like the noble thing to do.

Lyell and another of Darwin's peers, Joseph Dalton Hooker, did not agree with that view. They had been aware of Darwin's theory for years and were not prepared to withhold their knowledge of Darwin's priority. They proposed a compromise: to present Wallace's essay together with some of Darwin's unpublished writings at a meeting of the Linnean Society of London. Modern opinions about these arrangements can be strong indeed, especially

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among those who think Wallace was unfairly treated. This is another mid-20th century view. According to the standards of the time, however, the arrangement was fair. Wallace had sent his essay without asking for it to be kept private. The conventions of the day allowed Darwin or Lyell to publish it. Wallace was always accorded the honour of being the co-discoverer of natural selection and never tired of expressing his gratitude and satisfaction.

These brief writings of Darwin and Wallace offered the first statement of how species came into existence by natural means, yet they made remarkably little impact. Urged to bring out a reduced overview of his massive work in progress, Darwin spent 13 months condensing his 20 years of study into a single volume. This was published on 24 November 1859 as *On the Origin of Species*.

The book was immediately controversial and widely reviewed and discussed. Darwin came in for a great deal of ridicule and abuse. The implication that human beings must have evolved from earlier species was particularly objectionable to many, as was the revelation that no divine guiding hand was needed; species evolve on their own.

But Darwin also gained strong support especially from members of the younger generation of naturalists, such as Thomas Henry Huxley (today always referred to as Darwin's bulldog, but not known as this in his lifetime). Darwin's mass of evidence, ranging from embryology and vestigial organs to geographical distribution, and his arguments in favour of evolution were overwhelming.

Despite its baptism of fire, *On the Origin of Species* almost single-handedly convinced the international scientific community that evolution was a fact. In his 1889 book *Darwinism*, Wallace wrote of the revolution Darwin effected: "this totally unprecedented change in public opinion has been the result of the work of one man, and was brought about in the short space of twenty years!".

The theory of evolution has come a long way since. Today we think of it in terms of genes and DNA, but Darwin and Wallace had no idea of their existence. It was only in the 1930s and 1940s that genetics was incorporated into evolutionary theory. Even now, new discoveries are shaking up our understanding, but at the core of the modern theory remains Darwin's idea of descent with modification.

Today evolution has many critics outside the scientific community, especially in the US, where a significant percentage of the population are creationists. What is forgotten is that the scientific debate over evolution was over by the 1870s and has never again been a matter of serious dispute. ■

AN IDEA OF ITS TIME

Many strands of 19th century science, from concern about how a burgeoning human population could support itself to the discovery of strange fossils of long-dead animals, led Darwin and others to ideas about how species arise, evolve and go extinct

1795

Erasmus Darwin, Charles's grandfather, foreshadows Darwin when he writes: "Would it be too bold to imagine that all warm-blooded animals have arisen from one living filament... with the power of acquiring new parts"

1798

The doom-mongering *An Essay on the Principle of Population* by Thomas Malthus warns of the dire consequences of unrestricted population growth. It is a key influence on Charles Darwin

1809

French naturalist Jean-Baptiste Lamarck publishes *Philosophie Zoologique*, outlining his idea of evolution according to a "complexifying force"

1809

Charles Robert Darwin is born in Shrewsbury, UK, the fifth of six children in a prosperous family

1813

French zoologist Georges Cuvier publishes an *Essay on the Theory of the Earth*, setting out his idea that new species appear after catastrophes such as floods

1823

Alfred Russel Wallace is born in the village of Llanbadoc near the border of England and Wales, the seventh of nine children

1831

Darwin sets sail on HMS Beagle for a survey of South America. The voyage lasts five years

1837

Darwin sketches the first "tree of life" in his notebook to explain the evolutionary relationships between species

1848

Wallace departs for an expedition to Brazil. On the return journey four years later, a fire destroys many of his specimens

1858

Wallace conceives of his theory of how species adapt to a changing world. On 1 July both Wallace's and Darwin's ideas are presented at the Linnean Society of London

1859

Darwin's *On the Origin of Species* is published and becomes the object of much ridicule and abuse

1860

Debating evolution at Oxford, Bishop Samuel Wilberforce asks Thomas Huxley, a champion of Darwin's ideas, if Huxley's monkey ancestors were on his grandmother's or grandfather's side

1870

Evolution comes to be accepted as fact by most of the international scientific community

EVOLUTION VS CREATION: THE GREAT 1860 DEBATE

Darwin’s ideas were always going to cause controversy among those who championed a literal interpretation of the biblical story of creation. That first came to head in a notorious debate in Oxford, the year after *On the Origin of Species* was published, in which evolution’s most fervent adherent, Thomas Huxley, went head to head with the Bishop of Oxford, Samuel Wilberforce.

“THE proprieties of the Association have been outraged.” So wrote civil servant Arthur Munby in his diary on 1 July 1860. And no wonder: the previous day, at the annual meeting of the British Association for the Advancement of Science in Oxford, there had been a most ungentlemanly discussion.

An American called John Draper had suddenly become the meeting’s hot ticket. His subject, Darwin’s evolutionary theory, was of wide and topical interest. *On the Origin of Species* had been published only seven months earlier, and emotions were running high.

But Draper wasn’t the attraction: word was that evolution’s fiercest opponents, including the Bishop of Oxford, Samuel Wilberforce, were planning to make a stand.

Only the library in the University of Oxford’s new museum could hold the anticipated crowd, and even this grand hall needed extra seating to accommodate the throng. A troupe of carpenters set to work, and the air filled with sawdust and the sound of frenetic hammering.

It could have been a one-sided debate: Darwin was not there – he was unwell – and the prime defender of evolution, Thomas Huxley, was not planning to attend. However, he relented the day before, when accused of deserting the cause.

The hall was packed. A few sceptics spoke first, including the president of the Royal Society. Then Wilberforce rose to great applause and proceeded to argue that humans must have been specially created, rather than evolving from non-human animals, because the idea was a central pillar of Christianity. At the end of his argument, according to the following week’s edition of *The Press*, he asked the famous question: would Huxley prefer a monkey for his grandfather or grandmother?

Huxley’s response was double-edged. Respectful, but not giving any ground, he referred to Wilberforce as an “unscientific authority” but paid homage to the bishop’s intellect. “If I had to choose between being descended from an ape or from a man who would use his great powers of rhetoric to crush an argument, I should prefer the former,” he declared. According to *The Evening Star* of 2 July, Huxley then went on to defend Darwin’s ideas “in an argumentative speech which was loudly applauded”.

In his own version of events, written in a letter to the marine zoologist Frederick Dyster in September, Huxley paints himself in an even better light. There was, he

> "As for your doctrines I am prepared to go to the Stake if requisite... I trust you will not allow yourself to be in any way disgusted or annoyed by the considerable abuse & misrepresentation which unless I greatly mistake is in store for you... And as to the curs which will bark and yelp – you must recollect that some of your friends at any rate are endowed with an amount of combativeness which (though you have often & justly rebuked it) may stand you in good stead – I am sharpening up my claws and beak in readiness."

THOMAS HENRY HUXLEY

writing to Charles Darwin on 23 November 1859 regarding *On the Origin of Species*, showing the fervour for the ideas set out in the book that earned him the name "Darwin's bulldog"

THE NATURAL HISTORY MUSEUM/ALAMY STOCK PHOTO

wrote, "inextinguishable laughter among the people" at his witty reply. "I believe I was the most popular man in Oxford for full four-and-twenty hours afterwards."

Others were not quite so impressed by Huxley's performance. Robert FitzRoy, captain of HMS Beagle during Darwin's all-important voyage, remained unconvinced by Huxley's arguments, and the archaeologist and biologist John Lubbock was left thinking Darwin's hypothesis was nothing more than the best on offer.

Indeed, when Joseph Hooker, assistant director of the Royal Botanic Gardens at Kew, related the day's events to Darwin, he grumbled that Huxley didn't "put the matter in a form or way that carried the audience" so he'd had to do it himself. "I smashed [Wilberforce] amid rounds of applause ...Sam was shut up – had not one word to say in reply and the meeting was dissolved forthwith."

Wilberforce didn't remember it that way. "I think I thoroughly beat him," he wrote to archaeologist Charles Anderson three days later. The physicist Balfour Stewart agreed. "I think the Bishop had the best of it."

Victory, it seems, lay in the eye of the beholder. After a decade delving through the documents, Frank James, historian at London's Royal Institution, came to the conclusion that the popular view of Huxley's victory may have arisen only because Wilberforce was not well-liked, a fact missing from most accounts. "Had Wilberforce not been so unpopular in Oxford he would have carried the day and not Huxley."

But what does the official record say? Very little. The association's report for 1860 makes no reference to the discussion at all. "The British Association had a gentlemanly ethos. And these were most ungentlemanly goings-on," says James.

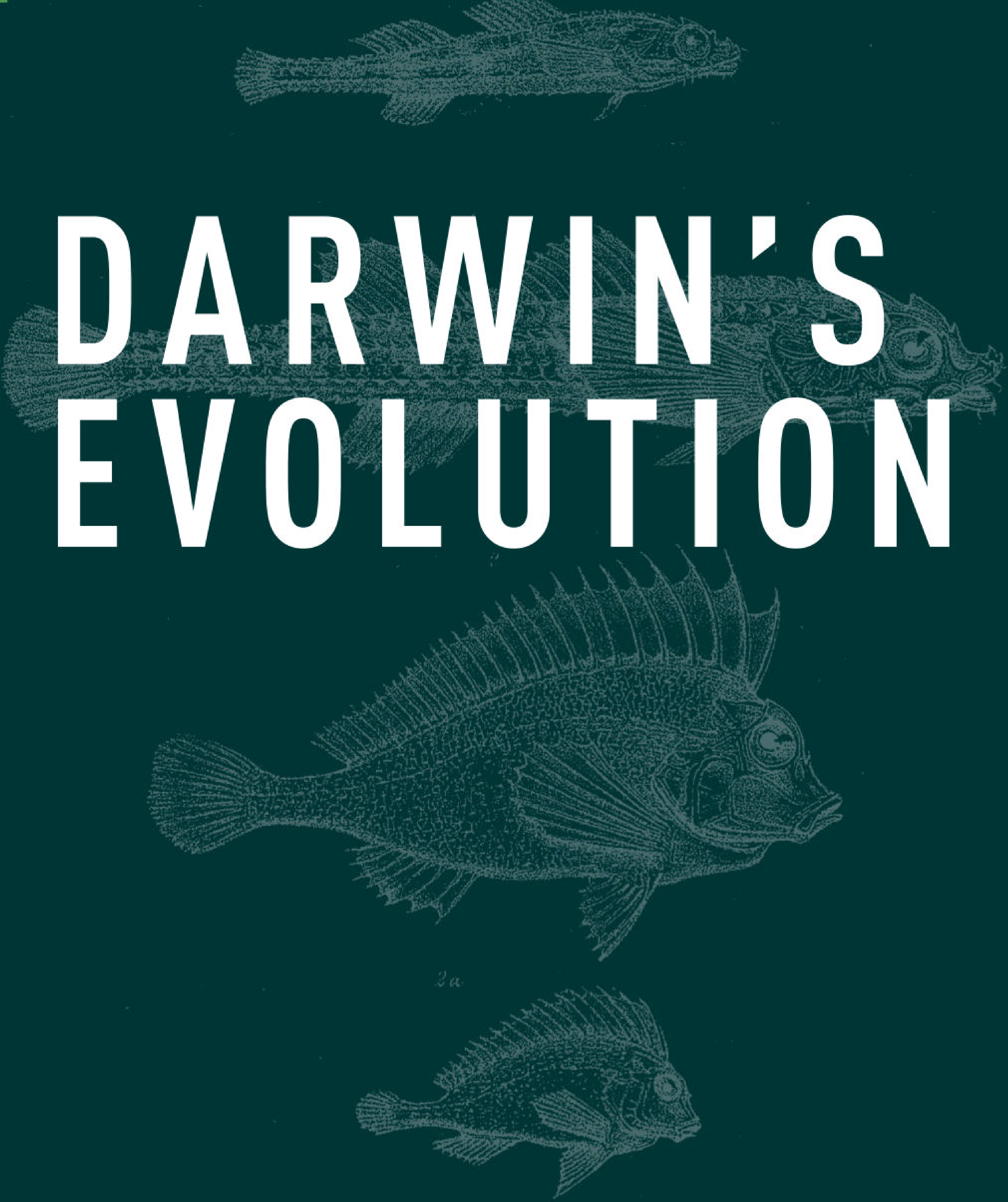
In the end, the gentlemen of the British Association suppressed as much information about the debate as possible, never realising the significance of their decision. The story of Huxley's victory only really took hold 20 years later – when it suited the cultural climate. "In the 1880s there was a split developing between religion and science," James says. "In the 1860s there really wasn't one."

But, without any official record of the meeting to counter their claims, scientists looking to establish their authority were able to refer back to the debate as the moment when science defeated religion: the battle, they declared, was already won.

"You see it referred to as an enormously important event when, at the time, it quite clearly wasn't," James says. But by turning this local discussion into a universal myth, men and women in the late 19th century contributed to the process of separating science from Christian belief. ▮

CHAPTER 2

DARWIN'S EVOLUTION



Modern ideas of genetics and heredity were unheard of when *On the Origin of Species* was published. Yet astoundingly, the basic principles Darwin set out in the book remain how we understand evolution today.

Evolutionary biologist Steve Jones kicks off our examination of the details of Darwin's theory by revisiting what this seminal work tells us.

ON THE ORIGIN OF SPECIES, REVISITED

PROFILE
STEVE JONES

Steve Jones is a geneticist and evolutionary biologist, and emeritus professor at University College London. He is author of popular books including *The Language of the Genes* and *Almost Like a Whale: The Origin of Species updated*

PREVIOUS PAGE: THE NATURAL HISTORY MUSEUM/ALAMY STOCK PHOTO
RIGHT: RAYMOND BIESINGER

UNIQUE among scientific disciplines, evolutionary biology finds its roots in a popular book by a single author. The grey-bearded genius presented a new and radical view of existence: that life has changed over time and space, in part through a simple process called natural selection.

Charles Darwin called his work "one long argument". To a 21st-century reader it seems lengthy indeed, with only a single illustration to enliven its 150,000 words. But Darwin was a clear thinker and the book is an impressive piece of advocacy, moving from the familiar – how animals on farms have changed – to the less so, embryos and instinct included.

Darwin also shows how what might seem to be problems for his argument, such as the uncanny perfection of complex structures like the eye, are in fact part of the solution, and how apparent weaknesses in his case – the incomplete nature of the fossil record included – can easily be explained. Now and again he was wrong, as when, unaware of Gregor Mendel's work on genetics, he claimed that inheritance is based on the mixing of bloods, but mostly he was right.

Darwin described the process of evolution as "descent with modification". Today that might be rephrased as "genetics plus time". Offspring resemble their parents because they inherit DNA from them, ›

ON
THE ORIGIN OF SPECIES
BY MEANS OF NATURAL SELECTION
BY CHARLES DARWIN, M.A.,
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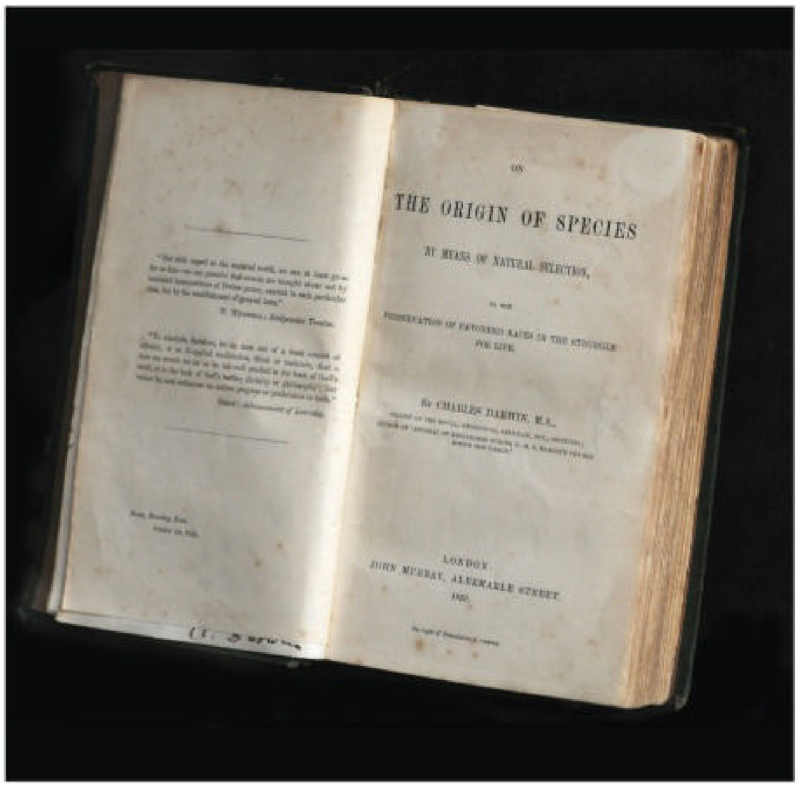
1859.

The version of *On the Origin of Species* that Darwin published in 1859 was much shorter than his original intention



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

By CHARLES DARWIN, M.A.

LONDON:
JOHN MURRAY, ALBEMARLE STREET.

DORSET MEDIA SERVICE/ALAMY STOCK PHOTO

but the copying process is not precise. Every round has errors, or mutations, and although they are individually rare – with perhaps one or two mutations in working genes each generation in humans – they can soon build up vast diversity. A copy of a copy is always imperfect, and for that reason alone, evolution is inevitable.

Darwin had a second insight. He saw that if a certain variant allows its carriers to survive, to mate and to pass on their heritage more successfully than others, in later generations it will spread. Such inherited differences in the chances of reproduction allow creatures to adapt to changing circumstances and can, in time, give rise to new forms of life. Natural selection, as he termed it, is a factory for making almost impossible things.

On the Origin of Species was written in something of a rush. When Darwin discovered that Alfred Russel Wallace had hit upon the very idea he had been cultivating since soon after his return from the Beagle voyage, he condensed and refined his plan for a much longer book and set out to bring his theory to a wide audience. The book is far shorter than that first scheme, but as a result it is much clearer – which is, no doubt, why it made such an immediate impact. Darwin apologised again and again for leaving so much out and spent much of the rest of his life filling in the gaps.

CHAPTER ONE:

VARIATION UNDER DOMESTICATION

In which Darwin uses examples from domestication to explore the causes of variability and the principles of selection

Farmers have been unwitting evolutionists since they began, as they have shaped the characteristics of domesticated species. Nowhere is the power of human selection more clearly seen than by the fireside. Dogs were domesticated around 16,000 years ago in China, perhaps for meat. Their ancestors were wolves – and the two still share the same scientific name, *Canis lupus* – but dogs have changed mightily since then. The breeders were ruthless, killing off the animals of which they did not approve. This selective death, combined with selective sex, soon subdivided dogs into a huge variety of forms.

Some kinds have been distinct for many centuries but most are less than 200 years old. In Darwin's childhood there were no more than 15 designated breeds. By the time *On the Origin of Species* was published, the number had risen to 50. It is now around 400. Many of today's varieties have gained a distinct identity in no more than 30 or so canine generations. Sometimes a single mutation sparks a new variety.

The Irish wolfhound stands a metre high and weighs as much as 30 Chihuahuas, but the difference in size between the two is due to a single gene, which comes in one form in the large animal and another in the small. Most divergence between breeds, however, involves many genes, unwittingly selected by breeders aiming to refine the characteristics of particular lineages. Were the various breeds of dog to run wild, they might be classified by an enthusiastic but naive naturalist as separate species. How could a Dobermann possibly belong in the same category as a Chihuahua?

Even so, in spite of some logistical difficulties with sex, crosses among dog breeds produce fertile offspring, which is one of the several definitions of what a species is. In the same way, the European grey wolf crosses freely with domestic dogs, which is why it shares its name. The pedigree dog clubs have laid out the case for Darwinism in a few short decades.

CHAPTER TWO;

VARIATION UNDER NATURE

In which Darwin considers individual differences and highlights the wide degree of variability within species upon which natural selection works

The natural world is full of variation. The number of animal species identified so far is in the millions and there are no doubt many more yet to be discovered. Of other kingdoms of life even less is known. Many habitats are almost unexplored. A scheme to classify waterborne microbes sampled from the Atlantic, Pacific, Baltic, Mediterranean and Black Sea revealed thousands of new families of genes. They are proof of the presence of vast numbers of as-yet-unknown forms of life in a habitat that comprises 99 per cent of the biosphere.

Darwin was fascinated by the diversity of existence. He realised that new species are usually generated from the variation within existing forms which, genetics has revealed, is astonishing in its extent. Intra-species variability is scrutinised by natural selection, which promotes particular traits in particular environments. Should a creature occupy two distinct habitats separated by space or time it may become subdivided into two forms unable to exchange genes: that is, into two species.

Sometimes, the boundary between species is shifting and unstable, in testament to the dynamic and ever-changing pressures brought by a changing environment. In North America, for example, the red wolf and the coyote – distinct as they are – have lived in the same kinds of places for many generations. Each has maintained its identity. In recent years, though, they have been forced closer together by human activity, and have begun to produce fertile hybrids. For them, the barriers to gene-sharing were not quite complete, and what became for a time two is sliding back to become one.

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See page 68 for more on the question of what a species is

CHAPTER THREE:

STRUGGLE FOR EXISTENCE

In which Darwin describes the competition in nature for limited resources

All species have the potential to increase vastly in number, given time – but they do not, because of lack of food or because of disease, predation or for want of a home. In Darwin's day, the romantic poets and much of liberal society were in denial about this struggle for existence. Now we accept it, but we often forget quite how unforgiving it can be.

For example, around 400 million pet dogs live easy lives in human households. In the many cultures where dogs are regarded as dirty or dangerous, several million more roam in feral packs, forced to scavenge. Their days are chaotic, unhealthy and short. Meanwhile wolves, which once roamed throughout the world's northern forests, have been squeezed out by humans. Europe now has only a few thousand left and there would soon be none if they were not protected. Both wolves and feral dogs were unlucky to come up against the most intractable enemy that nature has yet produced; and both are paying the price in the struggle for existence.

CHAPTERS FOUR AND FIVE:

NATURAL SELECTION AND LAWS OF VARIATION

In which Darwin explains how inherited differences in the ability to survive and reproduce have shaped nature, and explores the forces influencing the variation upon which natural selection works

Ten thousand years ago, much of North America was covered with ice. As the glaciers retreated, they scooped out an intricate landscape of low hills, small lakes and rushing streams. Slowly, sticklebacks moved in from the sea. They found two distinct kinds of place to live in and adopted two ways of life. In lakes, where most of the food was available in open water, they became › slim and active swimmers. In streams, where the shallow bottom was a better place to forage, they evolved to be robust and tough so as to grub around for food. Although they are not yet classified as distinct species, each form now prefers to stay in its own home and to mate with its own kind. Natural selection has worked to adapt the fish to the challenges they face, with only those individuals best suited to passing the test of survival getting the chance to hand on their genes.

As Darwin recognised, the entrance examination to the next generation has two papers. The first involves staying alive, but there is a second paper that turns on successful reproduction. It leads to what he called "sexual selection". Males of many species are forced to compete for the attention of females, and it pays a female to choose the best mate to father her offspring, the vessel of her own precious genes. This struggle for sex can lead to the evolution of bizarre structures such as the peacock's tail. Far from helping their bearers to stay alive, these sexually attractive traits are often a handicap. That may be why they work, for they indicate that those who bear them have what it takes to survive despite their costly sexual signal.

CHAPTER SIX:

DIFFICULTIES ON THEORY

In which Darwin considers organs of extreme perfection and other apparent stumbling blocks for his theory

The mammalian ear is a wonderful example of how evolution can craft what at first glance looks like the work of an engineer. Fish can pick up sound waves with nothing more than simple pressure sensors on their bodies because water is an excellent conductor. When animals moved onto land, though, they needed to amplify sound waves, feeble as they are in comparison. Reptiles and birds have a lever – a tiny bone – between the outside world and the sensory cells of the ear that does the job, but in mammals the lever is comprised of three small, interlocking bones that work far more effectively.

The tale of the mammalian ear is one of make do and mend, and of structures modified for a new and different end. The earliest fish had no jaws. These developed later from bony arches that once supported the gills. Another gill arch became the single amplifying lever found in reptiles and their avian relatives. As the ancestors of mammals appeared, the ear began to hijack other structures. First, the position of the hinge between the upper and lower jaw shifted, freeing one bone of the upper jaw and one of the lower. These became the other two bones of the middle ear, so we hear, in part, with what our ancestors chewed with. Fossils reveal the whole process with a succession of creatures with more and more complete middle ears as proof of natural selection's ability to build on a series of successful mistakes and to craft complicated organs of apparent perfection.

Darwin knew nothing of genes, and his chapter on inheritance is the weakest in the book, but we now have molecular probes which reveal that the same genes are active in the fish sensory system as in the human ear – proof that genetics and evolution have become branches of the same science.

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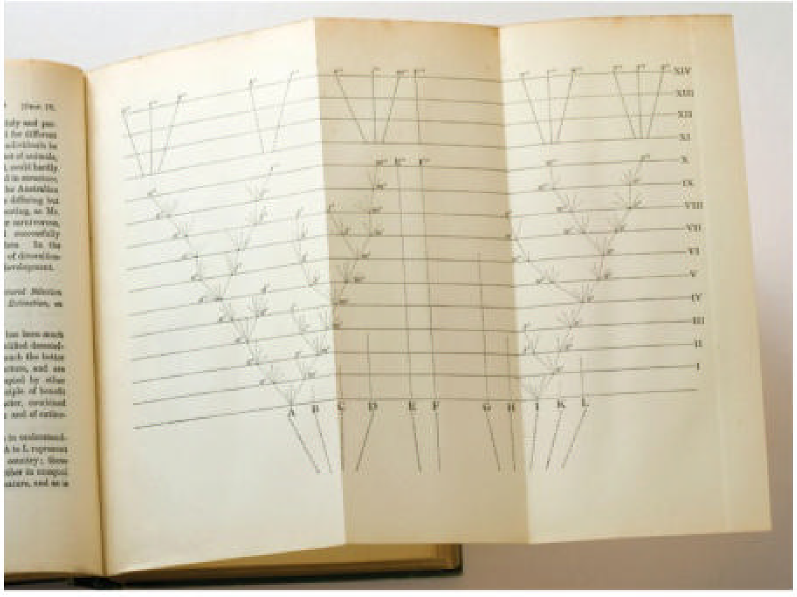
See chapter 3 for how modern ideas of genetics fit into evolution

That trade-off between sex and death is hard at work in a certain Trinidad guppy. In some streams the males

Branching tree of life illustration from *On the Origin of Species*. This is the only illustration in the book



DEREK CROUCHER/ALAMY STOCK PHOTO

have bright orange spots that entrance the females. In others there lurks a nasty predator that spots the spots and eats those who carry them. Here, the males have evolved to be dull. But move them to a stream without enemies and in just a few generations the bright spots reappear, testimony to the power of sex.

CHAPTER SEVEN:

INSTINCT

In which Darwin faces the issue of how behaviour might evolve

Dogs have long been used to hunt. Those with particular abilities – to track, to run, to recover corpses – were chosen as parents for the next generation. That history lives on in the instincts of today's breeds. Herding dogs such as border collies stalk sheep and do not bite them, but dogs bred to control larger animals, like corgis with cattle, go further and snap at their charges. Pit bull terriers are vicious creatures that can hold a bull – or a baby – by the nose. Can such psychological characteristics really evolve by selection?

Russian researchers in the 1950s showed that with selective breeding for tameness, once-wild silver foxes within a few generations began to wag their tails, bark and enjoy human company. Even their appearance altered, with new coat markings and floppy ears. After 30 generations they were completely tame. The brain, it seems, can evolve just as quickly as the rest of the body.

CHAPTER EIGHT:

HYBRIDISM

In which Darwin examines what keeps species apart

Species retain their identity because they live in different places, fail to have sex with each other or, if they do, produce infertile offspring. Hybrid sterility is due to genes, but because most species cannot be crossed it is hard to find out which ones are involved. Experiments with two kinds of Mexican fish show how little change is needed to keep species apart.

The platyfish lives in streams and is covered with elegant dark spots. In other streams nearby lives the swordtail, which looks much the same, although the males lack spots and have a long tail. The two species never cross in the wild, but can be persuaded to do so in the laboratory. Hybrids are spotty and survive reasonably well, at least in an aquarium, but if they are crossed in their turn to one of their own parents the next generation of offspring suffers a sinister fate. The small spots turn into lethal black tumours – and, in a macabre twist, males with these cancerous growths are much fancied by platyfish females.

A search through the DNA shows the problem. Cells have molecular brakes and accelerators that tell them when to divide, when to stop doing so, and when to die. In the hybrid fish, this control breaks down. The accelerator gene from one parental species refuses to respond to the command to slow down that comes from the other. As a consequence, the second generation hybrids die of cancer.

In an eloquent affirmation that evolution – shared descent – can unite quite distinct creatures, the overactive gene that leads to the problem in these fish is almost the same as the one which, when it goes wrong, causes skin cancer in us.

CHAPTERS NINE AND TEN:

ON THE GEOLOGICAL SUCCESSION OF ORGANIC BEINGS

In which Darwin considers the absence of intermediate varieties, explains why our palaeontological collections are full of gaps and describes how his theory can account for the pattern of succession from fossils to living forms

The geological record is like having just a few lines of a few pages of the history of the world. Much of it is incomplete, and because soft-bodied creatures are rarely preserved in the rocks some parts may be fragmentary at best. Since Darwin's day, however, vast numbers of fossils have been found across the world, and his concern that the geological record fails to support his theory now seems unduly pessimistic.

EVOLUTION IN A NUTSHELL

Darwin's ideas about evolution rest on three pillars: variation, inheritance and selection.

In the "modern synthesis" of evolution, which combines Darwinian theory with genetics, variation arises in the form of genetic mutations. DNA sequences change at random as the result of external forces, such as radiation, and internal ones, such as damage to DNA or RNA caused by highly reactive molecules called free radicals. Most of these changes are either neutral or detrimental to life, but a few lead to the adaptations on which evolution is built.

Mutations may occur in any cell, but only those in germ cells, such as eggs and sperm, are passed down the generations to produce genetically distinct individuals: this is the basis of inheritance.

One of Charles Darwin's greatest insights was the realisation that organisms tend to produce a variety of offspring, not all of which survive to reproduce. Natural selection weeds out those less well suited to their environment, he said, while fitter individuals survive and pass their traits on to their offspring. In this way, variation, inheritance and selection result in evolution, allowing life to adapt and new species to form as conditions change.

Today, evolution remains one of the most powerful ideas in science but, as with all good ideas, it is evolving – not least with the realisation that organisms take active roles in their own evolution.

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See chapter 3 for more on the "modern synthesis" of evolution

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See chapter 6 for more how evolution is itself evolving

Darwin could only guess at the age of each stratum by estimating the rate at which rock was worn away. Today we can date fossils directly by examining how their chemical elements break down with time. The first life has been traced back more than 3 billion years and the death of the dinosaurs to 65 million years ago. Some of the records of that immense period are impressively complete.

The Himalayas are full of fossils – not of mountain creatures but of those of the sea, for long ago their peaks made up the floor of the Tethys Ocean. The fossils include the antecedents of great whales. The bones of the earliest ancestor of all cetaceans are found in beds some 50 million years old. They belong to a creature that had four legs and a tail, lived on the shore and looked a little like a seal. Its ears, though, had a unique structure, now found only in whales.

The next prominent player, a million or so years later, "the swimming-walking whale" in Latin, looked like a 3-metre-long otter. Another million years on and the animal's nostrils had migrated up the snout and the pelvis moved away from the backbone. A further 5 million years saw the oceans inhabited by a long mammal with tiny limbs.

Then came a great split. The ancestors of the blue whale and its relatives – those that filter tiny creatures from the water – began to develop gigantic sieves within their mouths, while others retained the sharp teeth found in earlier whales and in today's killers. More recent deposits reveal the splits between dolphins and whales. A record that was once little more than an enormous gap has, with infinite labour and some luck, provided a complete history of the evolution of the largest animals that ever lived.

It has also given whales their rightful place – until not long ago quite obscure – within the family of mammals. Their earliest ancestors were close to those that gave rise to the hippopotamus. Whales, unique as they may seem, are hence members of a larger group that contains hippos, pigs, giraffes and cattle. DNA analysis backs up the record of the rocks. The whale's whole story has been revealed within less than half a century.

CHAPTERS ELEVEN AND TWELVE:

GEOGRAPHICAL DISTRIBUTION

In which Darwin demonstrates the importance of geographical barriers and climate change to explain the distribution of life as we see it today

Penguins are charming birds with between 17 and 20 species, depending on which classification is used. They take a variety of forms, ranging from the statuesque emperor found in the Antarctic, to the fairy penguin of Australia, just 1/20th its weight. Other penguins live in New Zealand, South Africa, South America and the Galapagos. They cannot fly (although the DNA suggests that albatrosses are among their closest relatives), so how did they reach such scattered places?

The oldest penguin fossils appear shortly after the demise of the dinosaurs around 65 million years ago. This ancestor of all living species lived in southern New Zealand and Marie Byrd Land, Antarctica, which were

> **“Darwin realised species adopt their evolved form only as they develop”**

at that time separated by less than 1500 kilometres. Already the ancestral penguins had almost lost their wings. Fossils and DNA each show that the penguins’ spread matches the advance and retreat of the ice. Starting around 35 million years ago, a series of ice ages made the Antarctic uninhabitable, and the birds retreated northwards as the glacier spread. In addition, icy currents swept some westwards, eastwards and closer to the equator.

After 10 million chilly years, the world warmed, cooled and warmed again, and the birds followed the retreating edge of the ice sheet into the far south. They left behind colonies scattered on cold-water shores across the globe. In the years since then, isolation and the challenges faced by each separate group have led to the diversity of penguins seen today.

CHAPTER THIRTEEN:

MUTUAL AFFINITIES OF ORGANIC BEINGS:

MORPHOLOGY: EMBRYOLOGY: RUDIMENTARY ORGANS

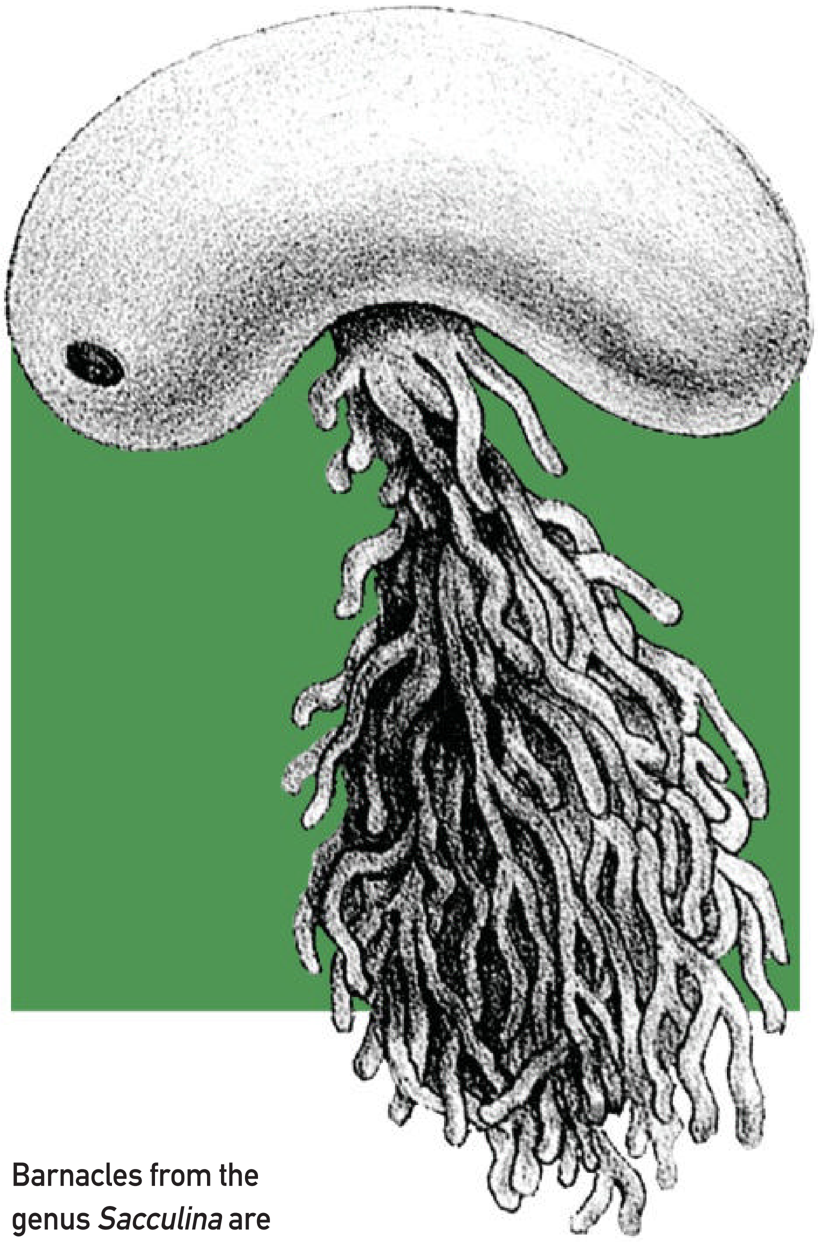
In which Darwin considers classification and shows how his theory can be used to organise the living world along evolutionary lines

As the past is the key to the present, so is the infant the key to the adult. Darwin realised that animals adopt the form which is adapted to their own evolved way of life as they develop. As a result, the deep relatedness between organisms might more readily be seen by comparing embryonic forms.

Darwin spent eight years working on barnacles, then an entirely obscure group but known to be related to crabs, insects and other jointed-limbed creatures. Adult barnacles vary in form from the familiar seashore kind to a sinister version that is an internal parasite of crabs and resembles a giant fungus. Whatever the divergence among the adults, though, the embryos are remarkably similar. They also resemble, to a lesser extent, the embryos of lobsters and crabs, and other jointed-legged creatures of the seas. All those in turn show affinities to the embryos of insects, a hint that butterflies have relatives on wave-battered shores, while that great group is in turn united in its earliest development with tapeworms and their relatives – creatures entirely different in their adult form. This shared identity, lost as the animals grow, shows how the embryo can reveal deep patterns of descent with modification, hidden as development goes on.

Darwin’s own classification of life – of groups within groups as evidence of a shared hierarchy of descent that encompasses not just barnacles and butterflies but birds and bananas – turned only on what he could see with the naked eye, or down the microscope. Now genes – the units of evolution – have come to the rescue, and they reveal whole kingdoms of existence quite unknown only a few decades ago.

The new tree of life is a direct descendant of the single sketch of shared descent that appears in *The Origin*. It is based on comparing the billions of DNA sequences now available from across the whole of existence. The affinity of whales with giraffes is a minor surprise when compared with discovery of the relatively close affinity of all animals to mushrooms, and the emergence of a whole new kingdom of single-celled creatures, the Archaea, which have a structure and a way of life entirely different from the bacteria that they superficially resemble. They may even have cooperated with them, in the early days of life, to provide the nucleated cells that build all plants and animals of today.



SCIENCE HISTORY IMAGES/ALAMY STOCK PHOTO

Barnacles from the genus *Sacculina* are parasitic castrators of crabs, and resemble other barnacles only in embryonic form

CHAPTER FOURTEEN:

RECAPITULATION AND CONCLUSION

In which Darwin expounds his "long argument" and addresses the "mystery of mysteries": why there are so many different species

A century and a half after *On the Origin of Species*, Darwin can be seen to have been triumphantly right about almost everything. Evolution is now no more "just a theory" than is chemistry and, like all other sciences, it provides a logical way of looking at the world. As he dared only to hope in that great book, light has been cast upon not just the worlds of plants and animals, but on ourselves and our origins.

Darwinism makes sense of what was once no more than a jumble of unconnected facts, and in so doing unifies biology. Modern psychology, ecology and more find their birthplace in the pages of his greatest work. A century-and-a-half on, evolution is as central to our understanding of life as gravity is to the study of the universe. The closing words of *On the Origin of Species* say it all:

"There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved." ▮

EVOLUTION ALL AROUND US

Although the basic ideas of variation, inheritance and selection underpinning *On the Origin of Species* are simple, their consequences are complex and profound. But evidence for evolutionary processes – for competition, adaptation and speciation – can be found everywhere in the natural world.

EVOLUTION has several facets. The first is the theory that all living species are the modified descendants of earlier species, and that we all share a common ancestor in the distant past. All species are therefore related via a vast tree of life. The second is that this evolution is driven by a process of natural selection or "survival of the fittest".

Darwin argued that all individuals struggle to survive on limited resources, but some have small, heritable differences that give them a greater chance of surviving or reproducing than individuals lacking these beneficial traits. Such individuals are said to have a higher evolutionary "fitness", and the useful traits they possess become more common in the population because more of their offspring survive.

Eventually these advantageous traits become the norm. Conversely, harmful traits are quickly eradicated as individuals that possess them are less likely to reproduce. Natural selection therefore works to create a population that is highly suited to its environment, and can adapt to changes.

When individuals compete for limited resources in their environment they are subject to ecological selection. However, useful traits are not only those that give a survival advantage, but also those that increase a plant or animal's chance of reproducing. These traits are subject to sexual selection.

Sexually selected traits can make an organism more

The subtly different beak forms of Galapagos finches bolstered Darwin's ideas about speciation

THE NATURAL HISTORY MUSEUM/ALAMY STOCK PHOTO

attractive to a potential mate, the peacock's tail for example. These are sometimes correlated to the health of an individual, and are therefore an honest badge of fitness. Another type of sexually selected trait gives males a physical advantage in outcompeting other males for mates, the stag's antlers for example. Sexual selection can even act at a molecular level.

Birds are particularly known for showy ornaments that attract mates, but also increase the chances of being spotted by predators. Other sexually selected traits include: lion's manes, great tit's or budgie's plumage, grouse mating rituals, insect love tokens, the height of human males and human hair, intelligence and facial features.

Over eons, and many generations, the process of slow evolutionary change can cause one species to evolve into another. But most new species form in a speciation event, when one species splits into two; a process that Darwin, as we've seen, called the "mystery of mysteries".

Allopatric speciation happens when a geographical change – a river changing course for example or a new mountain range – splits a species in two. Once separated, as happened to antelope squirrels on either side of the Grand Canyon in the US, the populations evolve independently, eventually becoming distinct and reproductively isolated.

Sympatric speciation occurs when new species emerge without separation, such as the 13 species of Galapagos finch or Africa's cichlid fish. These species adapt to different opportunities in the environment, and then cease to interbreed – perhaps due to some isolating mechanism. Rarely new species can also form through hybridisation, such as sunflowers.

Darwinian evolution is a slow, gradual process. But much of the fossil record hints at puzzling long periods of stasis, with scarcely any change. In 1972, evolutionary biologists Niles Eldredge and Stephen J. Gould argued instead that species, perhaps even communities, form suddenly in fits and starts of change. They called the theory punctuated equilibrium.

Like individuals in a population, species also struggle among themselves to survive, and most become extinct over time. Species can also die out in mass extinctions, such as the one that caused the demise of the dinosaurs. Today we may be in the throes of another mass extinction, caused by human overexploitation of habitats.

During his voyage on the HMS Beagle and throughout his life, Darwin gathered evidence that contributed to his theory of natural selection. In *On the Origin of Species* he presented support from the fields of embryology, geography, palaeontology and comparative anatomy. Darwin also found evidence for his theory in examples of convergent evolution, co-evolution and adaptive radiation.

Convergent evolution is when the same adaptations have evolved independently in different lineages of species under similar selection pressures. Today we see convergent evolution in species as diverse as: shark and camels, shrimps and grasshoppers, flamingos and spoonbills, marsupial and placental mammals and bioluminescent sea creatures. We also see it in the ears and teeth of mammals.

Co-evolution is when the evolutionary history of two species or groups of species is intimately intertwined. Examples include: the co-evolution of flowering plants and pollinators such as bees, lizards and moths; pocket gophers and their lice; humans and intestinal microbes; and the war our immune systems wage with the pathogens that attack us.

Adaptive radiation is the rapid speciation of one ancestral species to fill many empty ecological niches. Adaptive radiations are most common when animals and plants arrive at previously uninhabited islands. Examples of adaptive radiation can be found in: the Galapagos finches, Australia's marsupials, Hawaii's honeycreepers and fruit flies, Madagascar's carnivores and other mammals, New Zealand's birds and the prehistoric flying pterosaurs. ▮

CHAPTER 3

GENETICS AND EVOLUTION

It's all very well to say that species adapt and change, but what mechanism lies behind it? This is a problem that Darwin tried and failed to resolve.

The answer lay in a very different strand of research already going on elsewhere in the world. In the 20th century, what became known as genetics was the missing piece that completed the "modern synthesis" of evolutionary theory, as Peter Bowler explains.

DARWIN AND DNA

PROFILE
PETER BOWLER

Peter Bowler is a historian of biology at Queen's University Belfast and author of *Evolution: The History of an Idea*

OUR understanding of evolution today stems from the combination of two very different ideas. One came from a monk who studied pea plants in a Moravian monastery in the 1850s. The other came from a Victorian gentleman who spent five years as a naturalist on a voyage around the world, 20 years previously.

Although Gregor Mendel and Charles Darwin were alive at the same time, they never met and Darwin wasn't aware of Mendel's work. With hindsight, the union of the two men's work seems like a marriage made in heaven (or hell, if you're a creationist). In fact, for many years, it wasn't obvious that Mendel's studies of heredity had any relevance to Darwin's theory of evolution by natural selection. It would take nearly 60 years for this jigsaw to be pieced together and give rise to the "modern synthesis" of evolution, which framed Darwin's idea in terms of genetics.

How exactly did this new understanding arise? And why did it take so long?

The explanation starts with natural selection itself. According to this, only the fittest – the best adapted to the local environment – survive and breed, and in this way the population as a whole gradually transforms. The idea of evolution was already accepted by many biologists in the mid-19th century, but there was

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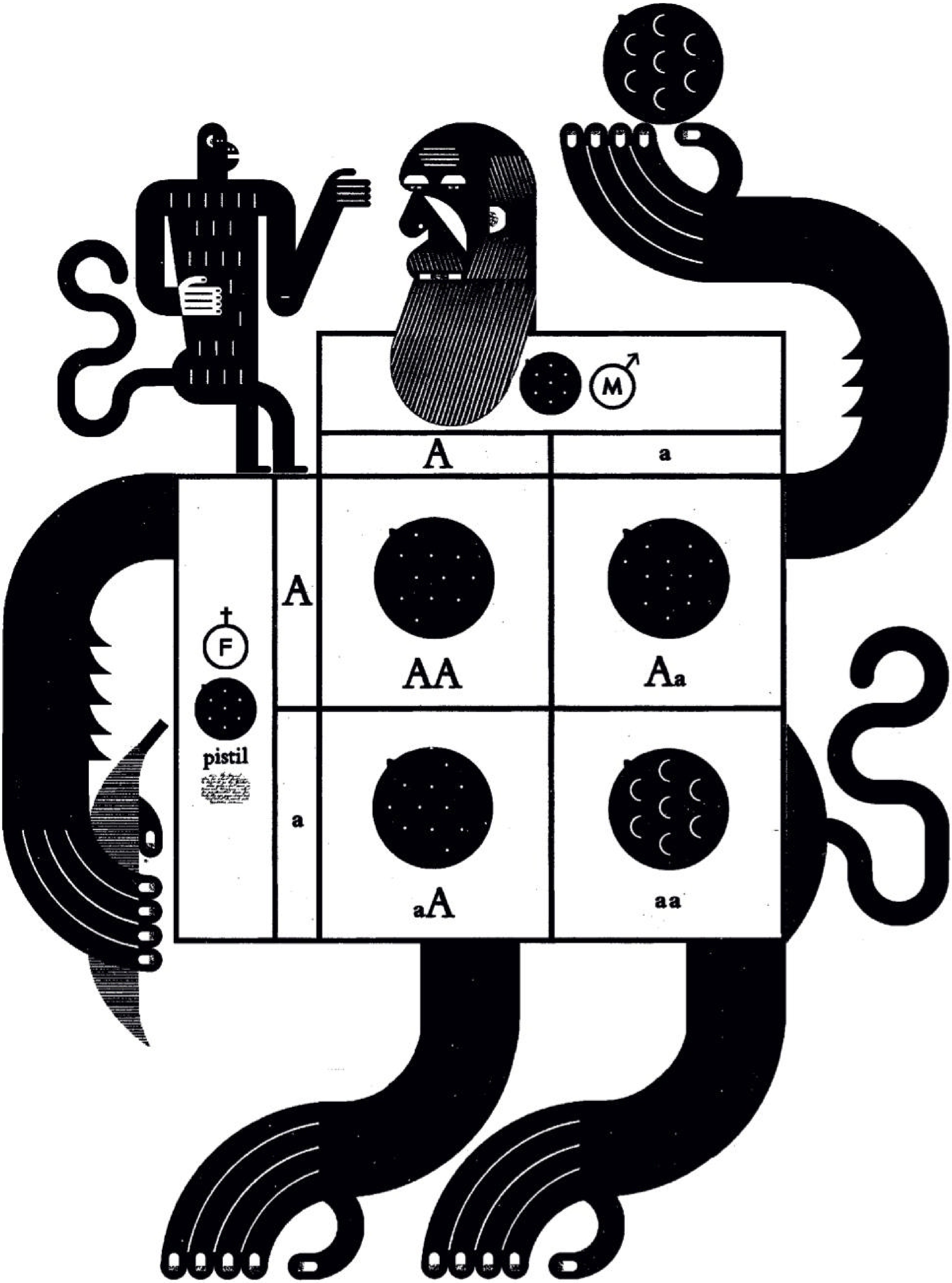
RIGHT: RAYMOND BIESINGER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considerable opposition to the notion that it happened by means of natural selection.

The plausibility of this mechanism rests on the assumption that beneficial characteristics are passed more or less intact from one generation to the next. But it was not clear how this might happen.

To explain heredity, Darwin proposed a hypothesis he called pangenesis. It posited that each organism produces particles called "gemmules", which transmit its characteristics to the next generation. Darwin suggested that the offspring develops from a mix of the parents' gemmules and thus exhibits a blend of their characters.

But the idea had a major flaw, seized upon by his opponents: blending would result in the useful characteristics of one parent becoming diluted as it mated with individuals that do not have those traits. Over successive generations these characteristics would gradually disappear. It was a problem no one was able to solve during Darwin's lifetime.

Unbeknown to Darwin and his compatriots, the key to solving this puzzle had already been found. Sometime in the 1840s, Gregor Mendel joined the friary at Brno, in what is now the Czech Republic. In the years that followed, he made detailed studies of how the characteristics of pea plants were passed from one generation to the next. He found that parents' traits were not blended in their offspring; rather, they were transmitted unchanged in predictable ratios. This led him to devise laws of inheritance, published in 1866 (see "Gregor Mendel and the birth of genetics", right).

No one imagined, though, that the characteristics Mendel studied in peas, such as flower colour, were of any general significance, and the work was largely ignored for decades.

Then in 1900, Mendel's laws were rediscovered by the botanists Hugo De Vries and Carl Correns. Through studying inheritance, each independently came to the view that an organism's characteristics are fixed units that are transmitted unchanged. Only later did they discover that Mendel had carried out similar work.

A new science of heredity emerged. First dubbed "Mendelism", it was soon christened "genetics" by the

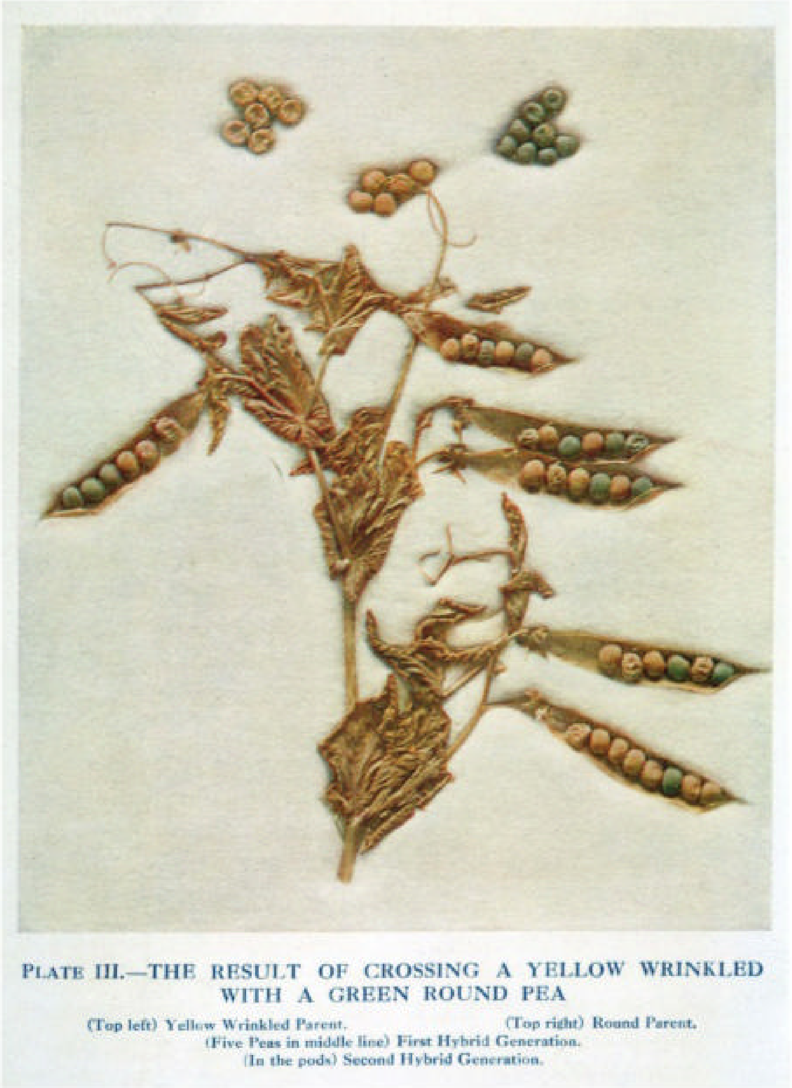


PLATE III.—THE RESULT OF CROSSING A YELLOW WRINKLED WITH A GREEN ROUND PEA

(Top left) Yellow Wrinkled Parent. (Top right) Round Parent.
(Five Peas in middle line) First Hybrid Generation.
(In the pods) Second Hybrid Generation.

Gregor Mendel's study of how the characteristics of pea plants were passed between generations led to the modern science of genetics biologist William Bateson, who translated Mendel's paper into English and was a key promoter of his work. Bateson derived the name from the Ancient Greek word "genesis", meaning "origin".

Mendel had expressed his laws in terms of characteristics transmitted from parent to offspring. The early geneticists were convinced that some material entity in the organism must encode that information.

Before long, the biologist Thomas Hunt Morgan had identified genes as units arranged along the chromosomes inside the cell's nucleus. Working on the fruit fly *Drosophila* in 1910, Morgan showed that the trait for eye colour could be traced to a specific place on the X chromosome. This led to a burst of discoveries about the links between different genes, and to the creation of genetic maps showing the positions of genes on chromosomes.

Morgan's research eventually won him a Nobel prize and confirmed that genes were the physical substance of inheritance. It would take another three decades, however, to discover that they were made of DNA and that each gene codes for a specific protein.

The concept of the gene seemed to be the missing piece in Darwin's jigsaw. It completed his picture of natural selection by showing that traits can't be blended away to insignificance, although this wasn't recognised immediately.

Genetics also solved another problem of Darwin's theory: the source of the variation within a population. Darwin's starting point was that any population naturally contains a variety of individuals, providing the raw material for natural selection. A key source of this variation was now shown to be mutation – spontaneous changes in the structure of a gene, leading it to code for something new. Such changes had been observed by Morgan and others as they traced the position of the genes on chromosomes.

Morgan himself came to believe that harmful mutations would quickly be eliminated from a population, thus recognising the negative side of natural selection. However, more work was needed to demonstrate how selection acted on genes to ›

GREGOR MENDEL AND THE BIRTH OF GENETICS

Gregor Mendel had an unlikely background for someone known as the founder of modern genetics, not least because he carried out his work 50 years before genes were actually discovered. Born in 1822 on a farm in what is now the Czech Republic, he joined the Augustinian friary at Brno and here carried out his work on heredity.

In the friary garden he bred thousands of pea plants, noting the presence of characteristics such as flower colour and wrinkliness of seeds. He found, for example, that when he crossed white-flowered plants with purple ones, the resulting plants weren't a light mauve, as might be expected if parental traits blended together, but appeared as either white or purple in fixed ratios.

These observations led him to devise the now famous laws of inheritance, published in 1866, which introduced the idea of dominant and recessive traits. This work went largely unnoticed until the turn of the century, when his ideas were incorporated into the new science of genetics.

The significance of Mendel's contribution is debated, however. His laws certainly helped to clarify how characteristics are transmitted from parent to offspring. But even Ronald Fisher, who used Mendel's ideas to create a genetic theory of evolution in the 1930s, suggested that Mendel's results were a bit too good to be true, perhaps "tidied up" by an overzealous assistant. And it is by no means clear that Mendel would have been a proponent of the theory that was based on his work. He expressed his ideas solely in terms of the transmission of characters from one generation to the next – there was no discussion of any mechanism.

Mendel eventually abandoned his studies when he became abbot at the age of 46. Little else is known about him as his correspondence and other personal papers were burned after his death.

CHRONICLE/ALAMY STOCK PHOTO

“Genetic selection is a creative force driving the adaptation of a species to its environment”

create positive evolutionary change.

According to Darwin, evolution is a slow process of gradual adaptation to the environment, in which most characteristics have, or once had, an adaptive function. So giraffes with slightly longer necks were able to reach leaves higher up, and thus gradually evolved longer necks through the process of natural selection. In contrast, many of the original geneticists saw evolution as something that happened in large jumps, or saltations, whereby new characteristics appear abruptly as the result of some internal rearrangement of an organism’s hereditary constitution. For example, a plant could suddenly start producing flowers of a colour not seen in its parents. The change would not necessarily have any adaptive benefit.

The early geneticists were attracted to Mendel’s laws precisely because they seemed to support these ideas. Morgan thought that “Nature makes new species outright” through a “sudden change of the germ”. Bateson saw no value in the Darwinians’ studies of continuous variation and resisted the claim that natural characteristics appear as a result of adaptive pressures on the species. By the same token, the saltation mechanism of change seemed to have no relevance to the process of natural selection.

These entrenched positions made it hard for anyone to suggest a way to reconcile the two approaches. But that changed in the 1920s, thanks to the new field of population genetics – the study of how certain genes within populations change over time.

The biologists Ronald Fisher, J. B. S. Haldane and Sewall Wright used sophisticated mathematical models to show that natural selection is able to enhance the frequency of any gene coding for a beneficial character, and eliminate those that are maladaptive.

This concept was developed in Fisher’s 1930 book *The Genetical Theory of Natural Selection* and in Haldane’s more popular *The Causes of Evolution* in 1932. That same year, Wright introduced the idea of an adaptive landscape, a map depicting all possible gene combinations and the resultant fitness of the organism.

Collectively, their work demonstrated that genes accounted for both the abrupt changes in characteristics sometimes seen in an organism’s offspring, and the continuous variation that Darwin had documented for large populations. These biologists showed that genetic selection is a genuinely creative force driving the adaptation of a species to its local environment, with continual mutation ensuring that the fund of variability is maintained. However, their theoretical models involved complex statistics and were hard to understand.

The gene-centred perspective of evolution only reached the wider scientific community in 1937, when Theodosius Dobzhansky published his *Genetics and the Origin of Species*, translating the mathematical formulations into terms that were more accessible. Dobzhansky’s work also expanded our understanding of how genetics enabled evolution, showing, for example, how new species could emerge when isolated populations changed to adapt to their local environment.

In 1942, the biologist Julian Huxley’s broad survey *Evolution: The modern synthesis* gave the new perspective a name. By the 1950s, this formulation had become dominant, although one key aspect would continue to be debated for decades to come.

More or less since its conception, Darwinian evolution was seen as an idea hostile to the Christian vision of nature as the product of some higher purpose.

In the US especially, creationist opposition to Darwinism took hold in the 1920s and has continued ever since.

←
Turn back to page 14 for more on early religious opposition to Darwin's theory

The founders of the modern synthesis wanted to present Darwinism as able to accommodate the belief that evolution has a built-in tendency to produce higher levels of organisation. Dobzhansky, for example, came from a Russian Orthodox background and wrote *Mankind Evolving* in 1962 to promote the idea that evolution had an ultimate purpose. Huxley also wrote prolifically to promote the idea of evolutionary progress. These authors presented ideas about the modern synthesis in a way that did not challenge traditional hopes and values too openly.

This, however, did not stop some of them being proponents of eugenics, the idea of enhancing the human population by eliminating "unfit" genes. Ronald Fisher, for example, devoted part of his 1930 book *The Genetical Theory of Natural Selection* to his hopes for improving the human race by this means. He even fathered eight children to further the cause. The dark reality of eugenics became clear in the early 20th century when several US states legislated to sterilise the "feeble-minded", and the Nazis took the idea to its ultimate, horrific extreme.

The quasi-religious portrayal of evolution as a means to an end would change in later decades, most notably with the publication of Richard Dawkins' *The Selfish Gene* in 1976 and his emergence as a leading proponent of the argument that nature has no ultimate moral purpose. Subsequent debates over the evolution of social behaviour and the emergence of altruism have taken place against the backdrop of an increasing tension between Darwinian evolution and religion – exactly what the founders of the synthesis hoped to avoid.

Despite these difficulties, the modern synthesis remains at the heart of our understanding of evolution today. It is itself evolving as advances in genetics, developmental biology and ecology broaden our understanding of the relationship between genes, organisms and the environment.

→
Chapter 6 has more on how our understanding of evolution is evolving today

The gene-centred view of evolution that emerged from the ideas of Darwin and Mendel is being transformed by the growing recognition that the environment in which the organism develops does play a role in shaping its characteristics, and may even affect the way traits are passed on to future generations. Discoveries in the field of epigenetics are showing that chemical tags that attach to genes to switch them on and off might be as important for development as the hardwired genetic code itself.

→
See page 77 for more on epigenetics

The modern synthesis was an idea for the 20th century. In the 21st, the story of evolution is set to acquire a sophistication that Darwin could only have dreamed of. ■

THE EVOLUTION OF GENETICS

The idea that species pass characteristics down through generations long predates Gregor Mendel's 19th-century studies of pea plants. But it was only with the discovery of DNA as the vehicle of heredity in the mid-20th century that modern genetics began to take off

SPANTELDOTRU/ISTOCK

5000 BC

Demonstrating some understanding of inheritance, humans worldwide begin to selectively breed more useful varieties of livestock and crops, including wheat, maize, rice and dates

400 BC

Greek philosophers contemplate the mechanisms of human inheritance. Aristotle believes that traits acquired during life, such as injuries, can be passed to offspring. He also develops the theory of "pangenesis", which attempts to explain how these traits are transmitted via particles called "gemules" to the reproductive cells

1859

Charles Darwin, himself a proponent of pangenesis, publishes *On the Origin of Species* – his explanation of evolution by natural selection. Darwin provides a plethora of evidence on how valuable traits become more common in a population, but does not provide any explanation for the mechanism of transmission of these traits

1866

Augustinian monk Gregor Mendel publishes his work on the patterns of inheritance in pea plants. His meticulous studies mark the birth of modern genetics. Mendel's findings escape the notice of other researchers for over three decades

1882

Chromosomes are discovered by German biologist Walter Fleming, and named with the Greek prefix meaning "colour" because they become stained when cells are dyed

1902

Mendel's research is rediscovered by botanists in 1900. US and German cell biologists then independently notice the link between Mendel's "units of inheritance" and chromosomes. They conclude that hereditary information is contained within chromosomes

1905

The term "genetics" is created by British biologist William Bateson. The terms "gene" and "genotype" surface in 1909.

Sex chromosomes are discovered following work on butterflies and beetles

1910

US scientist Thomas Hunt Morgan is the first to discover a sex-linked trait, while studying the fruit fly *Drosophila*. The trait for eye colour, on the X chromosome, is also the first gene to be traced to a specific chromosome

1925

Studies show that X-rays can induce mutations in genetic material

1944

A trio of US geneticists revisit work from the 1920s and prove that, in bacteria, DNA is the hereditary material, and not protein as was previously suspected

1951

Clear X-ray diffraction images of DNA are captured for the first time by British researcher Rosalind Franklin

1953

Building on Franklin's work, biochemist James Watson and biophysicist Francis Crick at the University of Cambridge determine the now famous double-helix structure of DNA. They are awarded a Nobel prize in 1962 for their efforts

1961

Crick and South African geneticist Sydney Brenner report that trios of DNA bases – called nucleotides – each hold the instructions for one of the 20 amino acids that combine to form proteins

1973

US researcher Herb Boyer uses enzymes to cut DNA and splice it into bacterial plasmids, which then replicate producing many copies of the inserted gene. This heralds the dawn of genetic engineering

1978

Genetically modified bacteria produce the hormone insulin

1983

The gene for an inherited disorder (Huntington's disease) is mapped to a chromosome for the first time

1986

Kary Mullis in the US develops the polymerase chain reaction (PCR), which allows researchers to produce many millions of copies of DNA molecules in just a few hours

1990

The international Human Genome Project begins, with the goal of sequencing the entire human genetic code

Gene therapy is used successfully for the first time, to treat a 4-year-old girl with the rare hereditary immune disorder adenosine deaminase deficiency

1994

Flavr Savr tomatoes, genetically modified to have a long shelf life become the first GM product to go on sale in the US. GM tomato puree goes in sale in the UK in 1996

1996

Baker's yeast is the first (non-viral) organism to have its genome completely sequenced, followed by the worm *Caenorhabditis* elegans in 1998 and then the plant *Arabidopsis* and fruit fly *Drosophila* in 2000

2000

Completion of the draft human genome is jointly announced by US firm Celera Genomics and the Human Genome Project. The full sequence – comprising 30,000 to 40,000 genes – is completed in 2003

HOW GENETIC INHERITANCE WORKS

Mendel's work established the foundations for the modern field of genetics, but in the mid-20th century we began to understand its biochemical basis: how traits are encoded in DNA and passed from generation to generation.

DNA is the code of life, the means by which every living organism on Earth stores its genetic information. As a sexually reproducing organism, you get half of your DNA from each of your biological parents, and you will pass on a selection of half of it to any child you might conceive. DNA, which stands for deoxyribonucleic acid, is curled up and stored as chromosomes in the nucleus of every one of our cells. We also have some DNA inside the mitochondria that power our cells, while plants have extra DNA within the chloroplasts that enable them to photosynthesise.

The 1953 discovery of the shape of DNA, known as a double helix, is mainly credited to Francis Crick, James Watson, Rosalind Franklin and Maurice Wilkins. It is rather like a spiral staircase or twisted ladder in which every rung is a bond between matching "bases" on its two strands. But it was the work of many researchers throughout the decades that followed that determined what DNA codes for, how it is read, and how it is copied and passed on to new cells and future generations.

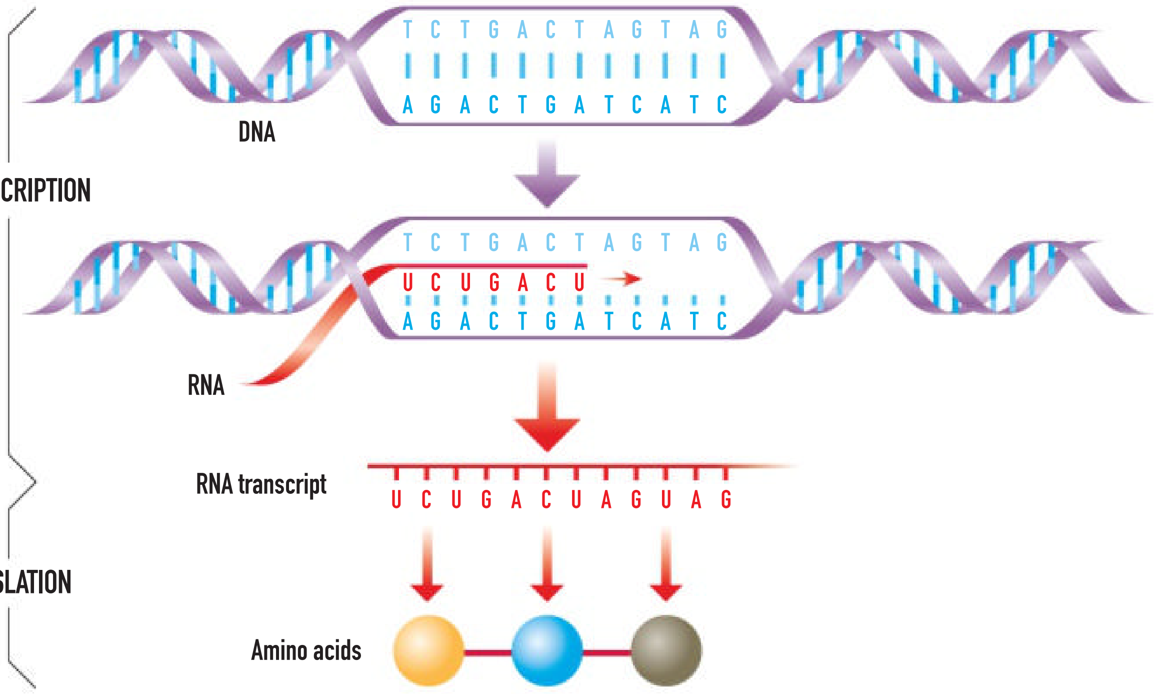
The order of DNA's chemical bases form the genetic code. These come in four types: adenine (A), guanine (G), cytosine (C) and thymine (T). The bases always pair up with the same complementary compound on the other strand of DNA: A with T, and C with G.

Three bases in a row together code for a specific amino acid, the basic building blocks of proteins. ACT, for instance, tells cells to make an amino acid called threonine. A sequence of such "codons" makes up a gene that can be many thousands of bases long. If the DNA bases are the letters of the genetic code, genes are the words, telling the cell's machinery how to make a vast array of proteins.

There is a lot of DNA packed in to every human cell. If you stretched it out, it would be almost 2 metres long. So your three billion bases, which are more than 99 per cent the same as everyone else's, need to be packaged up neatly. The coiled strands of your DNA are thus organised into chromosomes. Humans usually have 46 of these in each cell, 23 from each parent. The number varies in other animals: fruit flies have only eight and the black mulberry plant has 308, for example. Mitochondrial DNA is entirely inherited from an organism's mother.

What makes DNA so amazing is that it can copy itself, which allows all known organisms to function, grow and reproduce. Each strand of DNA in the double helix can serve as a template for duplicating its sequence of bases, enabling new cells to be exact copies of existing ones – although mutations often occur as a result of small errors in this process.

Humans and various other – but not all – organisms have two copies of almost every gene, one from each of their biological parents. Today, we know that the inheritance patterns of dominant and recessive traits



The DNA code consists of pairs of bases: C always pairs with G and A with T.

To make a protein, the code is transcribed onto a molecule of RNA – with U replacing T.

This is then used as a template to assemble amino acids, the building blocks of proteins

that Gregor Mendel observed are caused by different variants of the same gene, known as alleles.

These alleles can cause disease. For example, Huntington's chorea is a dominant disorder, meaning people only need to inherit one copy of the Huntington's allele to develop the condition. Cystic fibrosis, however, is a recessive disorder – a person must inherit two cystic fibrosis alleles to have the condition.

The combination of ideas about genetic heredity and Darwin's theory of evolution by natural selection into the "modern synthesis" revolutionised our understanding of biology, transforming it from a discipline defined by observations and specimen collecting to a field underpinned by unifying principles and a mathematical framework.

In the decades that followed, the structure and function of DNA was determined, and we now understand how genes work, how they are passed down the generations, and how they mutate and evolve.

We now know that, in addition to single-gene traits like cystic fibrosis in people or wrinkly seeds in peas, a large number of traits are governed by multiple genes. One human example is height.

In addition to this, many traits are even more complex, being governed not only by many different genes that each have a tiny effect, but also being influenced by the environment that we live in. Intelligence and obesity are two examples of these.

To unpick the role of genes, geneticists use sophisticated statistical methods. Calculating the heritability of a trait, by tracking it in a population, gives an idea of the degree to which variation in that trait is attributable to genetics, rather than environmental conditions. Twin studies enable researchers to further determine the extent to which genes might be responsible for certain traits. Genome-wide association studies can be used to sift through data to pinpoint genes that seem to be associated with certain characteristics.

As our understanding of genetics has advanced, we have been able to develop new scientific techniques based on genes. Genetic modification involves inserting new genes into an organism, to give it additional traits or abilities, such as pesticide resistance. Gene therapy has been developed as a treatment for some single-gene disorders, and works by administering functional copies of particular genes to people who have faulty alleles.

Until recently, modifying the DNA of humans and other organisms has been a difficult and laborious task, but new gene editing techniques such as CRISPR mean that we can now change genes much more easily. If these techniques can be made safe enough for use in people, they could lead to significant new medical treatments, but also open the door to human enhancement – genetic changes designed not to treat disease, but to improve our appearance or abilities. We might then be taking evolution into our own hands. ▮

CHAPTER 4

EVOLUTION MYTHS

While the basic principle of evolution is easily stated – that natural selection favours the retention of genetic mutations that confer “fitness”, or a survival advantage – the details of how that works can be fiendishly complex.

That, coupled with the controversy that evolution arouses in some religious circles, has led many myths and misconceptions to grow up. In this chapter, we look at some of the most prevalent and persistent.

Confronted with the marvels of the living world, it's easy to jump to the conclusion they cannot be the result of chance alone. But in fact, by harmful mutations and assembling beneficial ones, natural selection can over time produce results that appear utterly impossible at first glance.

MYTH: EVOLUTION'S OUTCOMES ARE IMPLAUSIBLY UNLIKELY

“THE chances that life just occurred are about as unlikely as a typhoon blowing through a junkyard and constructing a Boeing 747,” astronomer Chandra Wickramasinghe told a court in Arkansas in 1981 that was hearing an objection against a mandate that schools in the state should give equal weight to evolution and creationism. His colleague Fred Hoyle made the tornado version of this claim famous – proving that even very clever people can utterly misunderstand evolution.

A somewhat better analogy would be starting with a million junkyards, painstakingly testing the wreckage left in each one after the tornado to find the most flight worthy, making a million exact copies of that junkyard, unleashing another million tornadoes, running another series of exhaustive tests, and so on, until you produce some kind of machine – no matter how crude and un-Boeing-747-like – capable of flying at least a few yards.

To understand evolution, you need to appreciate three things. First, that the space of possibilities in which genetic variations take place is so vast that quadrillion-to-one chances actually happen all the time. Second that, while genetic mutation is random, which mutations survive often is not. And third, that the accumulation of one beneficial mutation after another can produce amazingly complex systems. Natural selection can be seen as a kind of improbability drive that – given enough time – makes the

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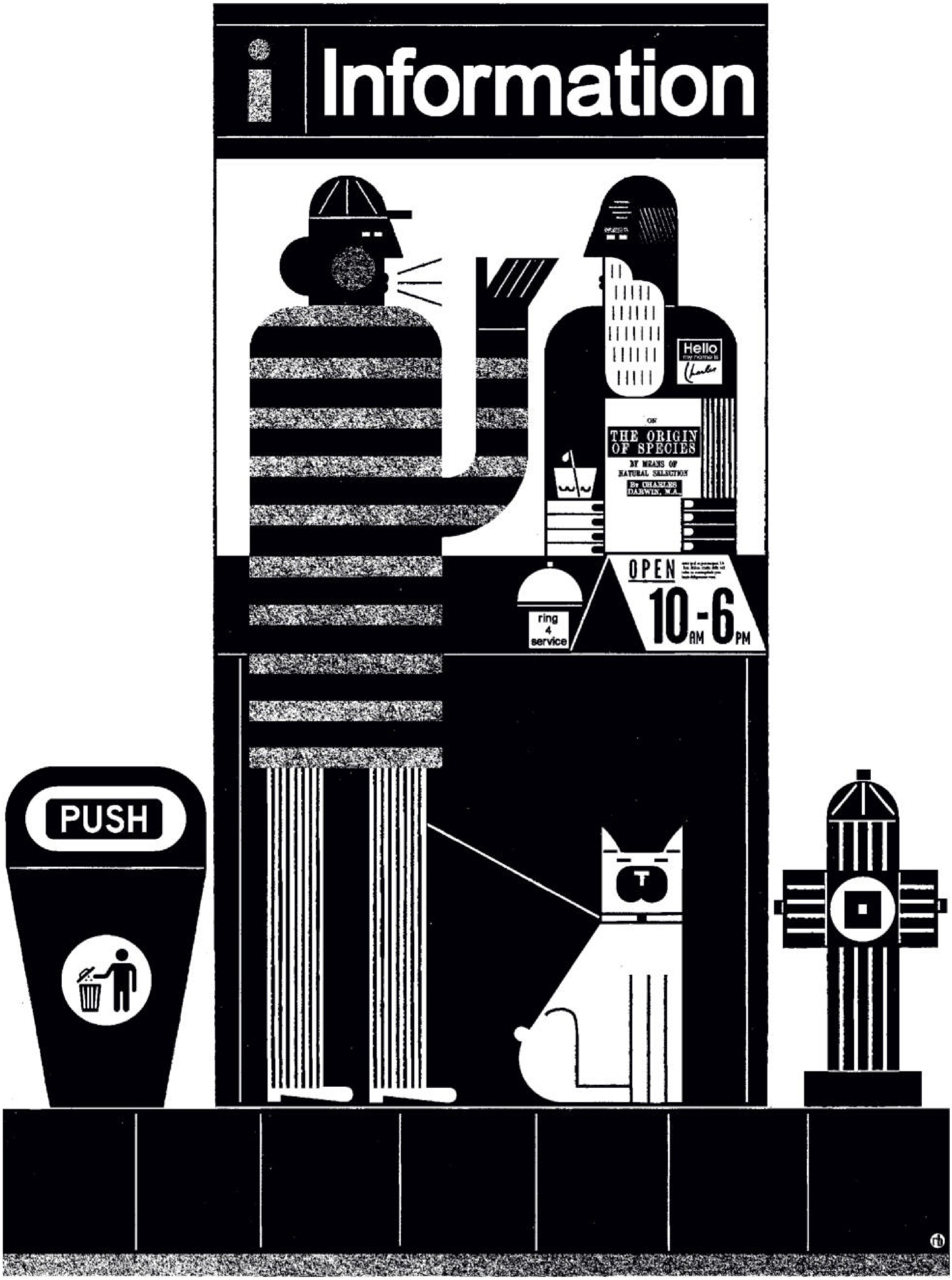
RIGHT: RAYMOND BIESINGER


Information
Hello
my name is
Charles
ON
THE ORIGIN OF SPECIES
BY MEANS OF NATURAL SELECTION
By CHARLES DARWIN, M.A.
OPEN
10AM-6PM
ring 4 service
PUSH

apparently impossible extremely likely.

If you pick even the simplest creatures alive today and calculate the odds of getting their genome by randomly shuffling DNA sequences, you'll find they are pretty astronomical. Even matching the sequence of the simplest virus is stupendously unlikely.

Does this prove evolution is impossible? Try this: get a pack of cards, shuffle it well and spread it out so you can see the sequence. Now try to generate the same sequence by shuffling another pack. The universe might end before you succeed. If shuffles are truly random, the chance of generating any particular sequence of 52 cards is 1 followed by 68 zeroes – and yet such an incredibly unlikely event happens each time any pack is shuffled.

In all living creatures, the "pack of cards" is constantly being shuffled. Damage to DNA or mistakes in replicating it generate random mutations, ranging from changes in single "letters" to duplications or deletions of huge chunks of DNA. The vast majority will be either harmful or neutral – only a few will be beneficial. But as the card example shows, even if all beneficial mutations are highly unlikely, this doesn't mean they cannot happen.

And what we don't see are all the failures: the countless numbers of creatures that died in the egg or in the womb, or hatched or were born with terrible defects, or fell victim to predators or disease because of some weakness. In the wild, most individuals die long before they get a chance to reproduce.

In fact, however, the odds of a beneficial mutation occurring are higher than you might think. One recent study of the *E. coli* gut bacterium puts the rate as high as 1 beneficial mutation for every 10,000 new bacteria.

That might not sound like much, but populations of many simple organisms can number in the trillions, with new generations appearing every hour or less. What really matters, though, is what happens after mutations appear. That's when natural selection kicks in. Each new organism's life is essentially a rigorous testing process. Those with a harmful mutation will tend to die out, while those with a beneficial mutation that gives them a competitive edge will thrive and produce more descendants. This means that beneficial mutations will become more common in a population, while harmful mutations disappear.

This process happens over and over again. If individuals with one beneficial mutation thrive and multiply, eventually another beneficial mutation will occur in one of them. Over time individuals with both beneficial mutations will come to dominate a population, making it likely for yet another beneficial mutation to appear in one of them.

What's more, in species that can swap genetic material, for instance by reproducing sexually, beneficial mutations that occur in separate individuals can be combined in their descendants. In this way, natural selection can create the astonishing organisms we see around us, the result of countless trillions of beneficial mutations slowly assembled over billions of years.

It's true that how the process got under way in the first place is still something of a mystery. We won't begin to know just how likely or unlikely the origin of life was until someone manages to get life to evolve from scratch in the lab or discovers life that originated independently, perhaps on another planet. What is clear, however, is that as soon as the first primitive entities capable of replicating themselves emerged, further evolution was inevitable.

And the more evolution there is, the faster it may become. In fact, evolution might produce "evolvability". For instance, as organisms evolve systems that can cope with a wide range of environmental conditions, further evolution might become more feasible – an idea backed by recent experiments showing that evolution can be speeded by varying the environment.

Such ideas remain controversial. What is indisputable is that while the end results of evolution might appear utterly impossible, once you understand the way in which natural selection can collect and distil the results of chance events, there's nothing impossible about it at all. ∎

MYTH: EVOLUTION IS ENTIRELY RANDOM

Just because the underlying process of genetic mutation is random doesn't mean the evolution's outcomes are. Natural selection is a rigorous testing process that filters out what works from what doesn't, driving organisms to evolve in particular directions.

EVOLUTION by natural selection is a two-step process, and only the first step is random: mutations are chance events, but their survival is often anything but. Natural selection favours mutations that provide some advantage, and the physical world imposes very strict limits on what works and what doesn't. The result is that organisms evolve in particular directions.

Consider any kind of creature that lives underwater and has to chase its prey, for instance. Random mutations will result in some offspring having different shapes. Those with shapes that allow them to move faster with less energy are much more like to survive and reproduce than those whose shapes slow them down.

The result is that all fast-swimming creatures evolve a streamlined shape, as we see in animals as diverse as squid, sharks and dolphins. It might look like the result of design, but it shows instead the power of natural selection, which can be thought of as a rigorous real-world testing process for evaluating the effect of different mutations.

Organisms do not always hang about waiting for a helpful mutation to occur. For instance, the parasite that causes sleeping sickness has thousands of spare genes for its coat proteins, which it mixes and matches to generate new coats faster than its host's immune system can keep up.

More controversially, a few biologists think some microbes may have evolved mechanisms for boosting the mutation rate in specific genes when they are struggling to cope with a changing environment, or for "storing up" variation for when it is needed. Even if such mechanisms do exist, however, all they do is produce random variation. Natural selection – the testing process – is what moves evolution in particular directions.

One consequence of this is that evolution tends to produce similar "designs" to meet similar problems, a phenomenon known as convergence. There are countless examples. Pterosaurs, birds and bats all evolved similar ways of flying. Tuna and some sharks use similar mechanisms to keep their swimming muscles warmer than the surrounding water.

Evolutionary convergence occurs at every level, from proteins to societies. An unusual antibody once thought to be unique to camels has a close equivalent in sharks, for instance, while naked mole rats form social colonies like those of ants and bees. ›

“If it started again, evolution might take different paths to reach similar results”

What this means is that if we could wind the clock back and let life evolve all over again, it might take very different paths but still produce organisms that, in some ways, resemble the organisms alive today. There would almost certainly be streamlined swimmers in the oceans and winged creatures in the skies. In fact, some argue that the evolution of intelligence is also virtually inevitable, though intelligent organisms could be very different from us.

Another phenomenon that means the same characteristics keep popping up in different places is called developmental bias. “You find some solutions evolving over and over again, not because they’re the best, but because the developmental system [of organisms] has the tendency to throw up certain variations,” says Tobias Uller at Lund University in Sweden.

It can be seen most clearly in domestic animals bred for a specific purpose. Many of them have floppy ears and curly tails along with shorter snouts and different coat colours compared with their wild ancestors. Yet, these characteristics have no obvious links to the qualities for which these creatures have been bred, such as tameness, milk production and meat yield. The mystery of so-called domestication syndrome was cracked when scientists homed in on a tiny cluster of stem cells in the developing embryo. These “neural crest cells” are involved in the development of a variety of tissues influencing things like face and ear shape and coat colour. They also give rise to the adrenal glands, which play a key role generating the fight-or-flight response that underpins tameness. Increase tameness by breeding for it, and the shorter snout and curly tail are dragged along for the ride.

Developmental bias could be behind a fascinating quirk of evolution called parallel radiation: the phenomenon in which a species in one location diversifies into several distinct forms and, independently, the same diversification occurs in a different location. The incredibly diverse cichlid fishes that live in Lake Malawi and Lake Tanganyika in Africa are one much-studied example of this phenomenon.

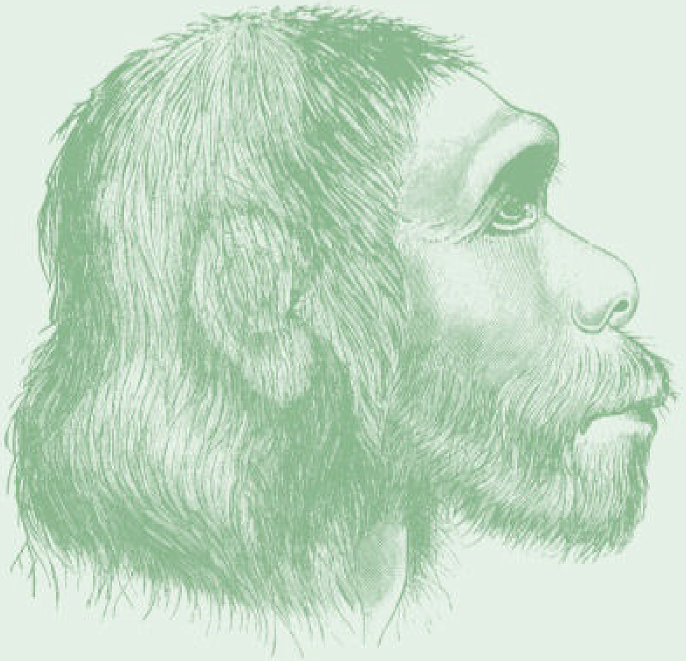
Despite directing evolution down certain tracks, developmental bias isn’t inherently limiting, says Uller, because it can promote variation that is more likely to be beneficial and therefore more likely to survive. It could help explain why cichlids are so diverse and similar bursts of evolution among all sorts of organisms, from the Galapagos finches studied by Charles Darwin to Australian marsupials.

Although evolution is not random in the senses described above, chance still plays a huge role. There are often numerous possible directions in which evolution can go. Take the Galapagos finches, which Darwin discovered had diverged into 13 separate species with beaks specialised for different foods. Why one group of birds took one route and not another probably depended entirely on chance mutations, in particular individuals, that affected beak size and shape.

What’s more, some mutations spread through a population or die out because of random genetic drift rather than natural selection. And chance events play a huge part too: if a huge asteroid hadn’t struck Earth 60 million years ago, dinosaurs might still rule the Earth.

So, while it is wrong to think that evolutionary theory implies that structures such as the eye and wing arose by accident, chance does play a role in evolution. ▮

MYTH: EVOLUTION IS JUST SURVIVAL OF THE FITTEST



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A phenomenon known as genetic drift working on the massively parallel mutations that underlie evolution means another process beyond natural selection kicks in: survival of the luckiest.

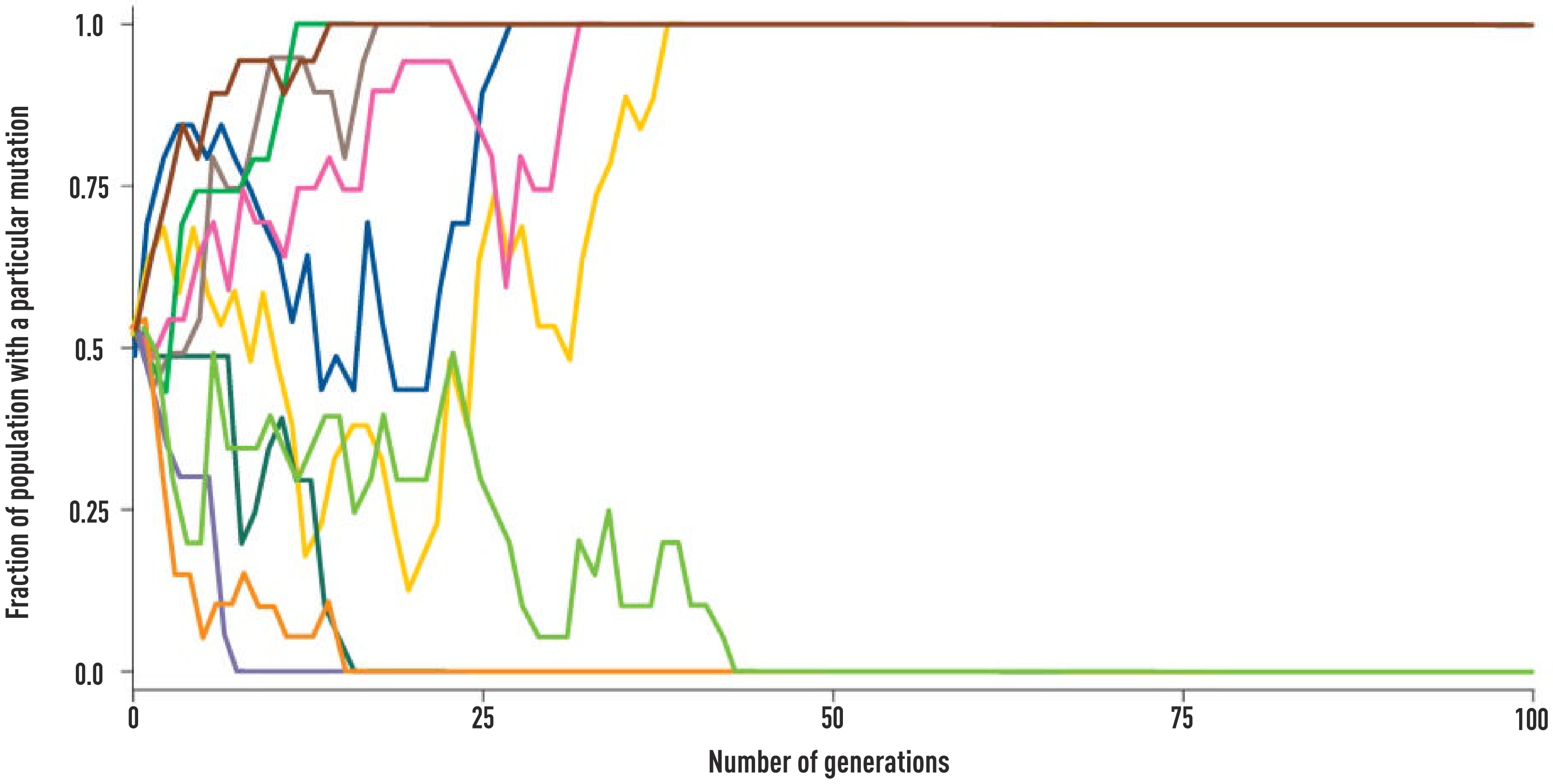
TAKE a look in the mirror. The face you see is rather different to that of a Neanderthal. Why? The unflattering answer could be for no other reason than random genetic drift. With features that can vary somewhat in form without greatly affecting function, such as the shape of the skull, chance might play a bigger role in their evolution than natural selection.

The DNA in all organisms is under constant attack from highly reactive chemicals and radiation, and errors are often made when it is copied. As a result, there are at least 100 new mutations in each human embryo, possibly far more. Some are harmful and are likely to be eliminated by natural selection – by death of the embryo, for instance. Most make no difference to our bodies. A few cause minor changes that are neither particularly harmful nor beneficial.

You might think that largely neutral mutations would remain restricted to a few individuals. In fact, while the vast majority of neutral mutations die out, a few spread throughout a population and thus become "fixed". It is pure chance – some just happen to be passed on to ›

Natural selection is not the only force in evolution. Mutations that have little or no effect on fitness can spread throughout a population or die out due to chance alone - the phenomenon known as genetic drift

With a population of just 10 "diploid" individuals - meaning each can have 0, 1 or 2 copies of any mutation - the entire population drifts to either having or not having the mutation within a few tens of generations. Depicted are 10 simulated runs of the population's evolution



more and more individuals in each generation.

Genetic drift is often explained in terms of a bag of tokens with equal numbers of two colours – 20 green and 20 yellow, say. A person draws a token, notes its colour and returns it to the bag, before repeating the process a further 39 times. These picks give a second "generation" of tokens – and chances are it contains more of one colour than the other: 17 green and 23 yellow, for instance. Repeating the process with this new population as a starting point will give a third "generation", which may be even more skewed in favour of yellow tokens. Eventually, the experimenter might randomly pick a generation containing all yellow tokens.

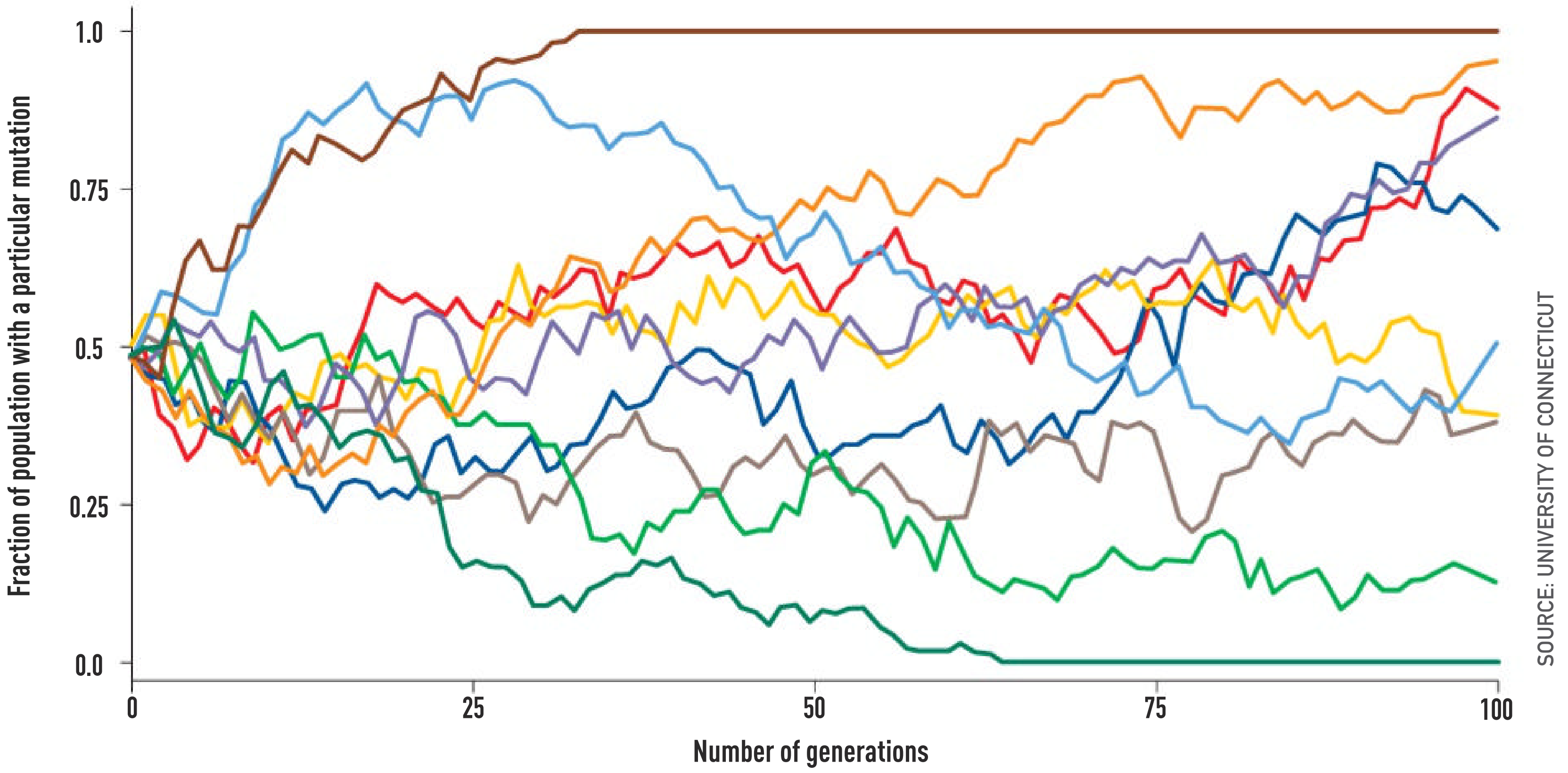
Although the likelihood of any neutral mutation spreading by chance is tiny, the enormous number of mutations in each generation makes genetic drift a significant force. Most changes in the DNA of complex organisms over time are due to drift rather than selection, which is why biologists focus on sequences that are similar, or conserved, when they compare genomes. Natural selection will preserve sequences with vital functions, but the rest of the genome will change because of drift.

Genetic drift can even counteract natural selection. Many slightly beneficial mutations can be lost by chance, while mildly deleterious ones can spread and become fixed in a population. The smaller a population, the greater the role of genetic drift: it would take countless generations for 1000 green and 1000 yellow tokens to "drift" into a population of 2000 green tokens, for example, but perhaps just a few generations for 10 green and 10 yellow tokens to become a population of 20 green tokens. Such outcomes can and do occur in nature, which shows how a population can lose genetic variability simply through chance.

Population bottlenecks can have the same effect. Imagine an island where most mice are plain but a few have stripes. If a volcanic eruption wipes out all of the plain mice, the island will be repopulated by striped mice. It's a case of survival not of the fittest, but of the luckiest.

Biologists have known about genetic drift for a century, but in recent years they realised that it could

With a population of 100, the genetic drift effect is less marked, with most simulated populations retaining a mixture of individuals with and without the mutation



be especially common in urban settings where roads and buildings tend to isolate organisms into small populations. A 2016 study of the white-footed mouse, *Peromyscus leucopus*, in New York supported the idea. Jason Munshi-South at Fordham University, New York, and his colleagues discovered that urban populations have lost as much as half of their genetic diversity compared with rural populations.

In 2019, Lindsay Miles at the University of Toronto Mississauga, Canada, and her colleagues published a review of evidence from about 160 studies of evolution in urban environments, in organisms ranging from mammals and birds to insects and plants. Almost two-thirds of the studies reported reduced genetic diversity compared with rural counterparts, leading the researchers to conclude that genetic drift must have played a role. “Genetic drift can definitely be a significant driver of evolution,” says Miles.

These findings have big implications, because populations lose their ability to adapt and thrive if they lack genetic diversity for natural selection to work on. Of course, genetic drift isn’t confined to urban settings, but given how much urbanisation is expected to grow, the extra threat it poses to wildlife is concerning. It highlights the need to create green corridors so that animals and plants don’t become isolated into ever-smaller populations.

Random genetic drift has certainly played a big role in human evolution, too. Human populations were tiny until around 10,000 years ago, and went through a major bottleneck around 2 million years ago. Other bottlenecks occurred when a few individuals migrated out of Africa around 60,000 years ago and colonised other regions.

There is no doubt that most of the genetic differences between humans and other apes – and between different human populations – are due to genetic drift. However, most of these mutations are in the nine-tenths of our genome that is junk, so they make no difference. The interesting question is which mutations affecting our bodies or behaviour have spread because of drift rather than selection, but this is far from clear. ∎

MYTH: EVOLUTION ALWAYS PROMOTES SPECIES SURVIVAL

"Survival of the fittest" can in fact be an entirely misleading description of evolutionary change: evolution sometimes results in initially well-adapted individuals or populations becoming less fit, and even occasionally going extinct.

THERE are several ways in which evolution can reduce the overall fitness of individuals or of populations. For starters, natural selection can take place at different levels: genes, individuals, groups. What promotes the survival of a gene does not necessarily increase the fitness of the individuals carrying it, or of groups of these individuals. For example, parasitic DNA elements, or transposons, can spread through a population even though they make their host organisms less fit. Transposons are one cause of genetic diseases such as haemophilia.

Similarly, selfish individuals may thrive at the expense of altruistic individuals in a group – making them the "fittest" – even though they make the group as a whole less competitive. Such cheaters can have disastrous consequences.

In 1932, J. B. S. Haldane suggested that this could even lead to the extinction of populations – a phenomenon called evolutionary suicide. Models and some experimental evidence suggest he was right. For instance, when nutrients run low, individual myxobacteria (slime bacteria) may come together to form a fruiting body to produce spores. Lab studies have shown that cheating myxobacteria that only produce spores and never help form the non-spore producing parts of the fruiting body can drive populations to extinction.

Genes capable of driving populations to extinction might have practical uses. Biologists are exploring the possibility of releasing engineered parasitic DNA into populations of malaria-carrying mosquitoes, for

The male peacock's tail is a survival drag

example. There is concern that something similar could happen accidentally. Fish that have been genetically modified to produce a growth hormone grow faster and larger, mature earlier and produce more eggs. But they are less likely to survive in the wild than unmodified fish. According to the Trojan gene hypothesis, a gene variant that produces such characteristics could spread rapidly through a wild population despite reducing individual fitness, and eventually drive the population to extinction.

Another way in which evolution can reduce a species' chances of survival is through the accumulation of detrimental mutations. Mutations provide the vital raw material for natural selection, so if the mutation rate is too low a population will not be able to evolve fast enough to keep up with environmental changes.

If, on the other hand, a population's mutation rate is too high, detrimental mutations may accumulate faster than natural selection can eliminate them. Eventually, the number of mutations can exceed the "error catastrophe threshold", again leading to the extinction of a population.

In theory, any species with a very small population could accumulate deleterious mutations faster than it can eliminate them. The problem is especially severe for asexual organisms such as the Amazon molly – an effect known as Muller's rachet. It is far less of a problem for sexually reproducing species because the exchange of genetic material between chromosomes can separate good and bad mutations. Some unlucky offspring get saddled with lots of nasty mutations and die out, while the lucky ones get hardly any.

In theory, a mutation catastrophe can also occur as a result of linkage. This refers to gene variants that are inherited together because they sit next to each other on a chromosome. Suppose a mutation that greatly increases the mutation rate somehow ends up next to a new mutation that greatly increases fitness. The immediate fitness benefits of the beneficial mutation will initially mask the deleterious effects of the "mutator" mutation, meaning both mutations will rapidly sweep through a population, ultimately with disastrous consequences.

Finally, it has long been recognised that the competition between members of the same species to reproduce – sexual selection – can favour traits that reduce a species' overall fitness. Male peacocks with the biggest and brightest tails might get the females' attention, but lugging around a heavy, conspicuous tail reduces their chances of survival.

Studies of threatened bird species suggest that sexual selection can indeed drive populations to extinction. Some biologists go so far as to blame sexual selection for the conspicuous consumption that threatens humanity's future.

According to the handicap principle, features such as peacocks' tails evolve precisely because they are disadvantageous. Consider an individual who is trying to signal to females how fit and strong he is. If the signal is easy to make, weaker males can easily cheat by making the same signal. But if making the signal is costly – such as growing a large, clumsy tail or giving away food – there's no way to cheat.

Proving that any of these phenomena have ever led to extinctions in the wild is far from easy, because any species to which this has happened are, of course, no longer around to study. The indirect evidence is growing ever stronger, though. ∎

GLOBALP/ISTOCK

"Use it or lose it" is a mantra that applies readily in the processes of evolution – when there's little selective pressure to become more complex, organisms can often seem to go backwards in what they are capable of.

MYTH: EVOLUTION ALWAYS FAVOURS COMPLEXITY

FOR all the glorious complexity it has produced, evolution often takes away rather than adding. For instance, cave fish lose their eyes, while parasites like tapeworms lose their guts.

Such simplification might be much more widespread than realised. Some apparently primitive creatures turn out to be the descendants of more complex creatures. For instance, it appears the ancestor of brainless starfish and sea urchins had a brain.

Nevertheless, there is no doubt that evolution has produced more complex life forms over the past 4 billion years. The tough question is: why? It is usually simply assumed to be the result of natural selection, but it seems complexity might actually initially arise when selection is weak or absent.

To see why this might be, suppose an animal has a gene that carries out two different functions. If mutation results in some offspring getting two copies of this gene, these offspring won't be any fitter as a result. In fact, they might be slightly less fit due to a double dose of the gene. In a large population where the selective pressure is strong, such mutations are likely to be eliminated. In smaller populations, where selective pressure is much weaker, these mutations could spread as a result of random genetic drift, as described in the previous section, despite being slightly disadvantageous.

The more widely the duplicated genes spread in a population, the faster they will acquire mutations. A mutation in one copy might destroy its ability to carry out the first of the original gene's two functions. Then the other copy might lose the ability to perform the second of the two functions. As before, these mutations won't make the animals any fitter – such animals would still look and behave exactly the same – so they will not be selected for, but they could nevertheless spread by genetic drift.

In this way, a species can go from having one gene with two functions to two genes that each carry out one function. This increase in complexity occurs not because of selection but despite it.

Once the genome is more complex, however, further mutations can make a creature's body or behaviour more complex. For instance, having two separate genes means each can be switched on or off at different times or in different tissues. As soon as any beneficial mutations arise, natural selection will favour its spread.

If this picture is correct, it means that there are opposing forces at the heart of evolution. Complex structures and behaviour such as eyes and language are undoubtedly the product of natural selection. But when selection is strong – as in large populations – it blocks the random genomic changes that throw up this greater complexity in the first place.

This idea might even explain why evolution appears to speed up after environmental catastrophes such as asteroid impacts. Such events would slash the population size of species that survive, weakening selection and increasing the chances of greater genomic complexity arising through non-adaptive processes, paving the way for greater physical or behavioural complexity to arise through adaptive processes. ▮

To survive, you don't have to be perfectly adapted, just as well adapted as your competitors. The apparent perfection of plants and animals is more a reflection of our poor imaginations than of reality.

MYTH: EVOLUTION MAKES PERFECTLY ADAPTED LIFE FORMS

The UK's red squirrel seemed perfectly well adapted to its environment – until the grey squirrel arrived

IT IS a theme repeated endlessly in wildlife documentaries: how perfectly animals are adapted to their environment. It is, however, seldom true. Take the UK's red squirrel. It appeared perfectly well adapted to its environment – until the grey squirrel arrived, and proved itself rather better adapted to broadleaf forests thanks, in part, to its ability to digest acorns.

There are many reasons why evolution does not produce "designs" that are as good as they could be. Natural selection's only criterion is that something works, not that it works as well as it might. The classic example of an evolutionary botched job is the panda's thumb, which it uses to grasp bamboo. "The panda's true thumb is committed to another role. So the panda must… settle for an enlarged wrist bone and a somewhat clumsy, but quite workable, solution," wrote Stephen Jay Gould in 1978.

As this example shows, evolution is far more likely to reshape existing structures than to throw up novel ones. The lobed fins of early fish have turned into structures as diverse as wings, fins, hoofs and hands. We have five fingers because our amphibian ancestors had five digits, not because five is necessarily the optimal number of fingers for the human hand.

Many groups simply never evolve features that might have made them even more successful. Sharks lack ›

“In terms of rounds of mutation and selection, humans are one of the least-evolved species”

the gas bladder that allows bony fish to control their buoyancy precisely, for example, and instead have to rely on swimming, buoyant fatty livers and, occasionally, a gulp of air. Similarly, mammals’ two-way lungs are far less efficient than birds’ one-way lungs.

Then there’s the if you don’t use it, you lose it effect of continual mutation. For instance, many primates cannot make vitamin C, because of a gene mutation. This mutation makes no difference to animals that get plenty of vitamin C in their diet. However, when the environment changes, such loss of function can make a big difference, as one primate, *Homo sapiens*, discovered on long sea voyages.

Evolution’s lack of foresight can produce inherently flawed designs. The vertebrate eye – with its back-to-front wiring and blind spot where the wiring goes through the retina – is one example. Later adaptations have compensated for these problems to a large extent, but once natural selection fixes upon a flawed, but workable, design, a species’ descendants are usually stuck with it.

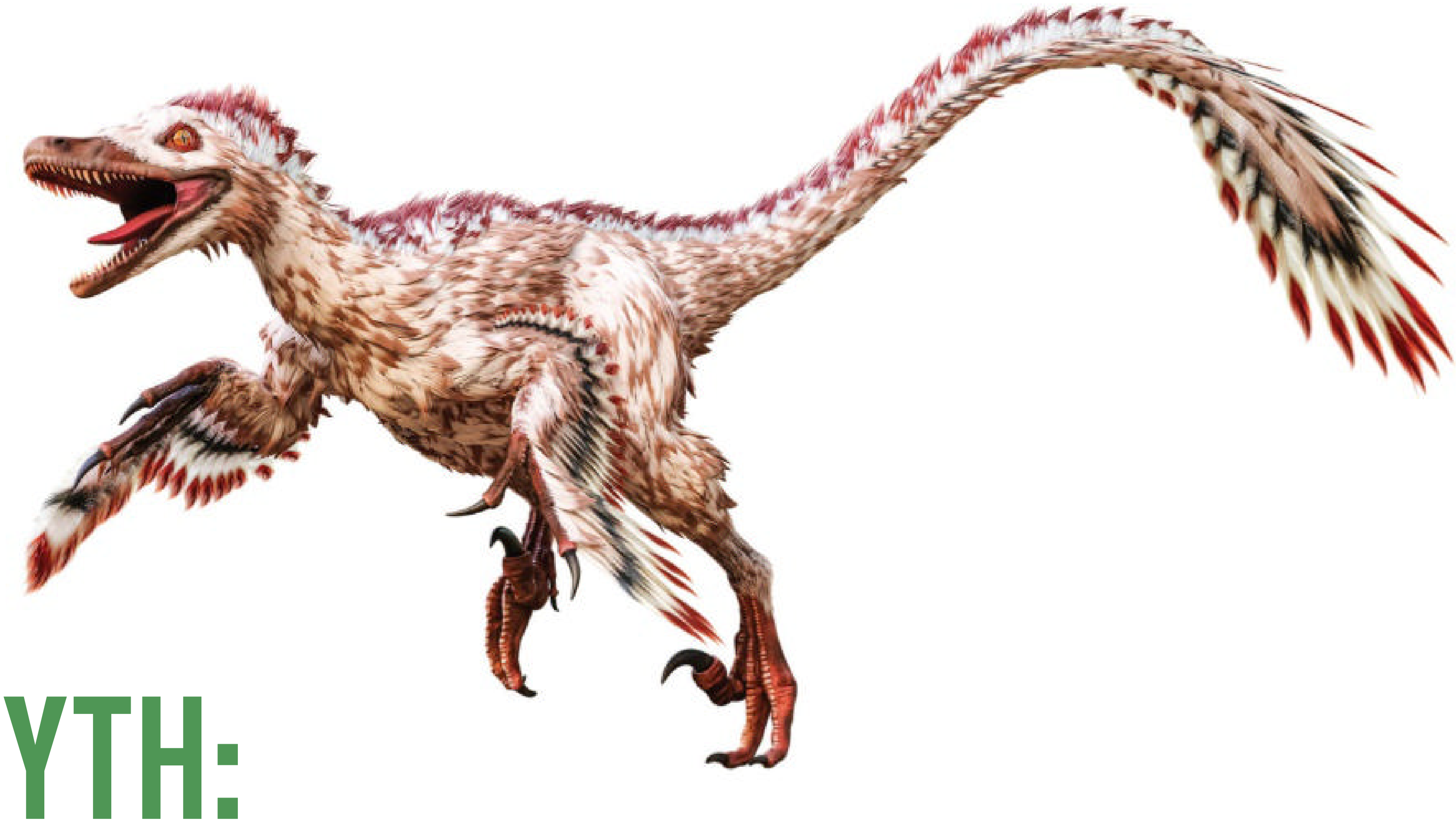
An organism’s fitness is also relative to its environment, which is usually changing. There is a constant arms race going on between predator and prey, parasite and host. Many species have to evolve continuously just to maintain their current level of relative fitness, let alone get fitter. As the Red Queen says in *Through the Looking Glass*: “It takes all the running you can do, to keep in the same place.”

Humans are not running fast enough. Evolving through natural selection is about time and numbers. The number of new mutations that appear, and the number of chances that natural selection has to eliminate the harmful and favour the beneficial ones, depends on the size of a population, the number of offspring each individual has and on the number of generations, among other things.

We might like to think of ourselves as the most “highly evolved” species but, in terms of how many rounds of mutation and selection we’ve undergone, we are one of the least evolved species.

In a decade, for example, bacteria can produce 200,000 generations – about the number of generations of humans there have been since our lineage split from that of chimpanzees. Billions of viral particles can be produced every day in the body of one infected human. It’s hardly surprising that in less than a human lifespan we’ve seen the evolution of new viral diseases such as covid-19 and HIV/AIDS, plus numerous antibiotic-resistant bacteria.

Although human evolution has sped up in the past 10,000 years, we are changing our environment faster still. As a result, instead of becoming better adapted, we are actually becoming less well adapted to the world we are creating. Think of the huge range of modern health conditions, from obesity and allergies to short-sightedness and drug addiction. Viruses and bacteria might approach perfection in their evolutionary ways, but we humans are at best a very rough first draft. ∎



MYTH: EVOLUTION HAS NO USE FOR HALF A WING

One lesson of natural selection is that, just as objects designed for one purpose can be used for another, so genes, structures and behaviours that evolve for one purpose can become adapted to do another.

Dinosaurs such as Velociraptor mongoliensis had feathers and probably small proto-wings, a precursor to those of birds

LIBRE DE DROIT/ISTOCK

EVER used a newspaper to light fires or mop up spills? Or stood on a chair to reach something? Just as objects designed for a specific purpose can be co-opted for something quite different, so features that evolved to do one task can be used for another – and often are.

But what use is half a wing? It's a question that those who doubt evolution first asked more than a century ago. When it comes to insects, rowing and skimming could be the answer. Stonefly nymphs have flapping gills for extracting oxygen from water. When standing on the water's surface, early insects could have used these gills for getting oxygen and propulsion rowing simultaneously. Some stoneflies still stand on the surface and "row" across water using their wings.

Over time, flapping could have replaced rowing as the main means of propulsion, allowing insects to skim across the water's surface: low levels of friction on › this scale mean proto-wings would not have had to generate much air flow to be useful for skimming.

As these proto-wings became more efficient and specialised, early insects may have taken further steps towards flying. While some skimming insects keep all six legs on the water's surface, faster skimmers keep just four legs or two legs on the water. This surface-skimming hypothesis concerning the evolution of insect flight shows how flapping gills could gradually have turned into wings while remained useful at every stage.

What about the wings of birds? In some dinosaurs, the scales covering their bodies evolved into hair-like feathers, most likely to insulate warm-blooded bodies or help keep eggs warm.

Those dinosaurs with feathers on their limbs might then have started to exploit the aerodynamic properties offered by feathers, perhaps gliding between trees or running faster along the ground. Fossils show a gradual transition from downy, hair-like feathers into the rigid flight feathers that form the key part of birds' wings.

Another idea that is gaining favour is that flapping forelimbs helped the ancestors of birds to run up steep slopes or climb trees – a technique many birds still employ today.

Without a time machine it is difficult to prove exactly what early birds or insects used "half a wing" for. But it is now clear that half a wing can have all sorts of uses. Indeed, there are numerous examples of physical structures and behaviours that evolved for one purpose acquiring another one, a process called exaptation.

Evo-devo – evolutionary developmental biology – is even starting to identify the precise mutations that underlie such changes. For instance, the forelimbs of the ancestor of bats turned into wings partly thanks to a change in a gene called *BMP2* that made its "fingers" far longer than normal.

The webbing between the extra long digits that makes up the bat wing is a reappearance of a long-lost feature: as embryos, all tetrapods initially develop webbed digits, a hangover from our fish ancestors. Normally, this webbing kills itself off at an early stage, but in bats this cell suicide is blocked.

Repurposing a structure does not have to involve the loss of the original structure. Reptilian jaw bones turned into mammalian ear bones, without the loss of the jaw. The neural circuitry that allows us to make fine limb movements may have been adapted to produce speech as well.

In fact, almost every feature of complex organisms can be seen as a variation on a theme. Switching off one gene in fruit flies, for instance, can turn their antennae into legs.

Sometimes just one aspect of a feature can be co-opted for another use. The first hard mineralised structures to evolve in our ancestors were the teeth of early fishes known as conodonts. Once the ability to form hard hydroxyapatite had evolved, it could be exploited elsewhere in the body and may have been the basis of the bony skeletons of all vertebrates.

As these examples show, there are all kinds of routes by which structures and behaviours that evolved for one purpose can contribute to new structures and abilities. Just because it is not immediately obvious how something as complex as a bacterial flagellum evolved does not prove it did not evolve.

An even more interesting question than what half a wing is good for is whether some features cannot evolve because half of them really would be useless. Such thought experiments might not prove anything, but they can be fun. ▮

It's a common assumption that all characteristics of plants and animals are adaptations that have arisen through natural selection. In fact, many are neither adaptations nor the result of selection at all.

MYTH: EVOLUTION EXPLAINS ALL OF NATURE

WHY DO so many of us plonk ourselves down in front of the telly with a microwave meal after a tiring day? Because it's convenient? Or because TV meals are "the natural consequence of hundreds of thousands of years of human evolution"?

Stop laughing. You've probably made similar assumptions. For just about every aspect of our bodies and behaviour, it's easy to invent evolutionary "Just So" stories to explain how they came to be that way. We tend to assume that everything has a purpose, but often we are wrong.

Take male nipples. Male mammals clearly don't need them: they have them because females do and because it doesn't cost much to grow a nipple. So there has been no pressure for the sexes to evolve separate developmental pathways and "switch off" nipple growth in males. Some people claim the female orgasm exists for the same reason as male nipples, though this is a far more controversial idea.

Then there's our sense of smell. Do you find the scent of roses overwhelming or do you struggle to detect it? Can you detect the distinctive odour that most ›

KANGAH/ISTOCK

Not every behaviour is a consequence of evolution people's urine acquires after eating asparagus? People vary greatly when it comes to smell, largely due to chance mutations in the genes that code for the smell receptors rather than for adaptive reasons.

Yet other features are the result of selection, but not for the trait in question. For instance, the short stature of pygmies could be a side effect of selection for early childbearing in populations where mortality is high, rather than an adaptation in itself.

Another reason why apparent adaptations can be side effects of selection for other traits is that genes can have different roles at different times of development or in different parts of the body. So selection for one variant can have all sorts of seemingly unrelated effects. Male homosexuality might be linked to gene variants that increase fertility in females, for instance.

A non-adaptive or detrimental gene variant can also spread rapidly through a population if it is on the same DNA strand as a highly beneficial variant. This is one reason why sex matters: when bits of DNA are swapped between chromosomes during sexual reproduction, good and bad variants can be split up.

Other features of plants and animals, such as the wings of ostriches, may once have been adaptations but are no longer needed for their original purpose. Such "vestigial traits" can persist because they are neutral, because they have taken on another function or because there hasn't been enough evolution to eliminate them even though they have become disadvantageous. Take the appendix. There are plenty of claims that it has this or that function but the evidence is clear: you are more likely to survive without an appendix than with one.

So why hasn't it disappeared? Because evolution is a numbers game. The worldwide human population was tiny until a few thousand years ago, and people have few children with long periods between each generation. That means fewer chances for evolution to throw up mutations that would reduce the size of the appendix or eliminate it altogether – and fewer chances for those mutations to spread through populations by natural selection. Another possibility is that we are stuck in an evolutionary catch-22 where, as the appendix shrinks, appendicitis becomes more likely, favouring its retention.

Wisdom teeth are another vestigial remnant. A smaller, weaker jaw allowed our ancestors to grow larger brains, but left less room for molars. Yet many of us still grow teeth for which there is no room, with potentially fatal consequences. One possible reason why wisdom teeth persist is that they usually appear after people reach reproductive age, meaning selection against them is weak.

For all these reasons and more, we need to be sceptical of headline-grabbing claims about evolutionary explanations for different behaviours. Evolutionary psychology in particular is notorious for attempting to explain every aspect of behaviour, from gardening to rape, as an adaptation that arose when our ancestors lived on the African savannah.

Needless to say, without solid evidence, claims about how, for instance, TV dinners "evolved" should be taken with a large pinch of salt. ▮

The non-appearance in nature of certain "phenotypes" such as wheeled animals, flying plants or zebras with machine guns suggests there are limits to evolution's creativity. In fact, the lesson might be the reverse: those just aren't very good solutions to life's problems.

WHY DON'T WILDEBEEST HAVE WHEELS?

"From so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved." That was how Charles Darwin described the incredible diversity of life forms generated by evolution.

And it's hard to gainsay him. Evolution exists because living things vary: each member of a species is subtly different to every other one. Those that are better suited to their environments are more likely to breed and pass on their genes, and so their favourable traits become more common in the population. Given enough time, this slow process can create wonders like gigantic blue whales, cooperative honeybees and towering sequoias. Evolution has produced animals that live more than 10 kilometres under the sea and bacteria that can handle doses of radiation that would kill a person many times over.

Yet some things just don't seem to turn up. Wheeled animals are a classic example – the evolutionary biologist Stephen Jay Gould discussed them in his 1983 book *Hen's Teeth and Horse's Toes* – but there are ›

WHY EVOLUTION IS SMARTER THAN YOU

There are plenty of animals that seem, at first glance, to be evolutionary mistakes; that appear to have evolved obviously disadvantageous traits. Yet on closer inspection, it often turns out that, as the biochemist Leslie Orgel famously said, evolution is cleverer than you are.

Take the Australian night parrot (*Pezoporus occidentalis*). As the name indicates, it is nocturnal, which you might think would mean it can see well in the dark. However, in June 2020, Vera Weisbecker at the University of Queensland, Australia, and her colleagues reported that its eye sockets were smaller than those of other parrots, as were its optic nerves. The study's accompanying press release said the bird "may not be much better at seeing in the dark than other parrots active during the day".

That may initially look like an evolutionary blunder, but Weisbecker's team doesn't claim anything of the kind. The researchers only had access to a skull, so they couldn't examine the bird's actual eyes, which might have adaptations to the dark. "What they suggest, based on the information they do have, is that its visual system is a kind of compromise between sensitivity to low light and also visual acuity," says Jennifer Hoyal Cuthill at the University of Essex, UK. That isn't a mistake – it is evolution balancing two competing problems.

Similarly, there is a popular idea that big spiders like the Goliath birdeater (*Theraphosa blondi*, pictured above), the largest in the world by mass, will "shatter" or "explode" if they fall even a few feet. This isn't only exaggerated, it is a misunderstanding of how such spiders live. Species like the Goliath birdeater are indeed vulnerable to falls. "If a large tarantula falls from a height, if it is unlucky enough to land upside down or with great impact, the exoskeleton could break open and the spider could bleed to death quite quickly," says Paula Cushing at the Denver Museum of Nature & Science in Colorado. However, she says that exploding and shattering are misleading descriptions.

More to the point, in practice, these spiders are rarely at risk of falling any distance at all, says Brent Hendrixson at Millsaps College in Jackson, Mississippi. "They're sit-and-wait predators and probably rarely venture to locations that would result in a fatal fall."

BLICKWINKEL/ALAMY STOCK PHOTO PREVIOUS PAGE: AARONAMAT/ISTOCK

“Biological evolution is the most unlimited process in the known universe”

many others. In a 2015 paper, Geerat Vermeij at the University of California, Davis, identified 32 combinations of traits that evolution has seemingly never produced. For instance, there are no rigid structures like coral reefs in fresh water, no plant-eating snakes and no flying plants.

It is tempting to invent reasons why these can’t exist, but Vermeij is reluctant to place such limits on evolution. “I think very few of these are what I would characterise as… forbidden phenotypes,” he says – a phenotype being the observable physical properties of a given organism. Given more time, evolution may well produce them.

Vermeij says we should imagine ourselves as evolutionary biologists living in the Ordovician Period, some 450 million years ago. “We couldn’t have conceived of some of the things that have actually evolved [since],” he says. “Things like flowers and flying insects. That demonstrates to me that evolution is very much a cumulative process, and what is now possible would not have been at that time.”

Jennifer Hoyal Cuthill at the University of Essex in the UK agrees. “Biological evolution is the most unlimited process in the known universe,” she says. “Its main striking feature is its ability to produce, as far as we’ve seen, infinite diversity. We haven’t run out of new animals. We have no idea where the edges of this space might be.”

Hoyal Cuthill says that many of the seemingly forbidden animals are examples of a kind of selective reasoning. Take the lack of plant-eating snakes. Many groups of animals have switched back and forth between eating meat and eating plants. Giant pandas are one such example: although they depend on bamboo, their ancestors were carnivores and their guts haven’t fully adapted to eating plants yet. No known snake has done this so far, which might imply that there is something about having this sort of body that is particularly suited to meat eating – or it might just be a coincidence. Hoyal Cuthill points out that snakes’ closest living relatives are lizards, many of which eat plants.

There may also be limits to our knowledge. For decades, it was thought that all spiders were primarily carnivorous. Then, in 2009, we discovered that a species called *Bagheera kiplingi* mostly eats plants.

Still, it is possible to go further and imagine much wilder scenarios. A 2007 paper by Timothy Shanahan at Loyola Marymount University in Los Angeles memorably asked: “Why don’t zebras have machine guns?” It argued that zebras would benefit from evolving machine guns to repel attacks by lions, but that they can’t because evolution has to proceed by intermediate steps, all of which must be advantageous – or, at least, not harmful. A machine gun is only useful when it is complete. As a functionless organ, it would just be hogging vital nutrients.

But there may not be as strong a limit here as it first appears, says Hoyal Cuthill. “Projectile weapons have frequently evolved. Archerfish use water as › a projectile weapon. Antlions use sand as a projectile weapon," she says. These animals are all ambush predators, so it may simply be that evolution doesn't favour projectile weapons in prey, because fleeing a predator is normally a better strategy than fighting it. The truth may not be that evolution can't fashion a rapid-fire projectile weapon for zebras, but rather that it doesn't do so because the existing solution – running away – works well enough.

This suggests that evolution hasn't even remotely reached its limits, and that over the next few hundred million years – and assuming humans don't cause a global extinction event – it might lead to animals and plants that are inconceivable to us today.

Vermeij argues that evolution is getting better at producing new things. "Organisms have, on the whole, become more energetic over time," he says. It is known, for instance, that the veins running through the leaves of flowering plants have become more densely packed over millions of years, meaning modern flowering plants can extract more energy from sunlight than their ancestors could 100 million years ago. Similarly, "the average metabolic rates of things like snails and clams and many other organisms have increased over time", says Vermeij.

The reason for that is competition, he says. "As organisms become more energetic, they also have more choice, and they have a greater opportunity to modify their environments."

Vermeij says one knock-on effect may be the evolution of general intelligence in multiple animal groups: not just humans and other primates, but cetaceans like dolphins, cephalopods such as octopuses and certain birds including crows and jays. "More brainpower and greater intelligence are themselves products of greater energetic investment, and are again favoured under most circumstances because they give the bearer greater choice," he says. The smartest organisms on Earth may be getting smarter over the ages.

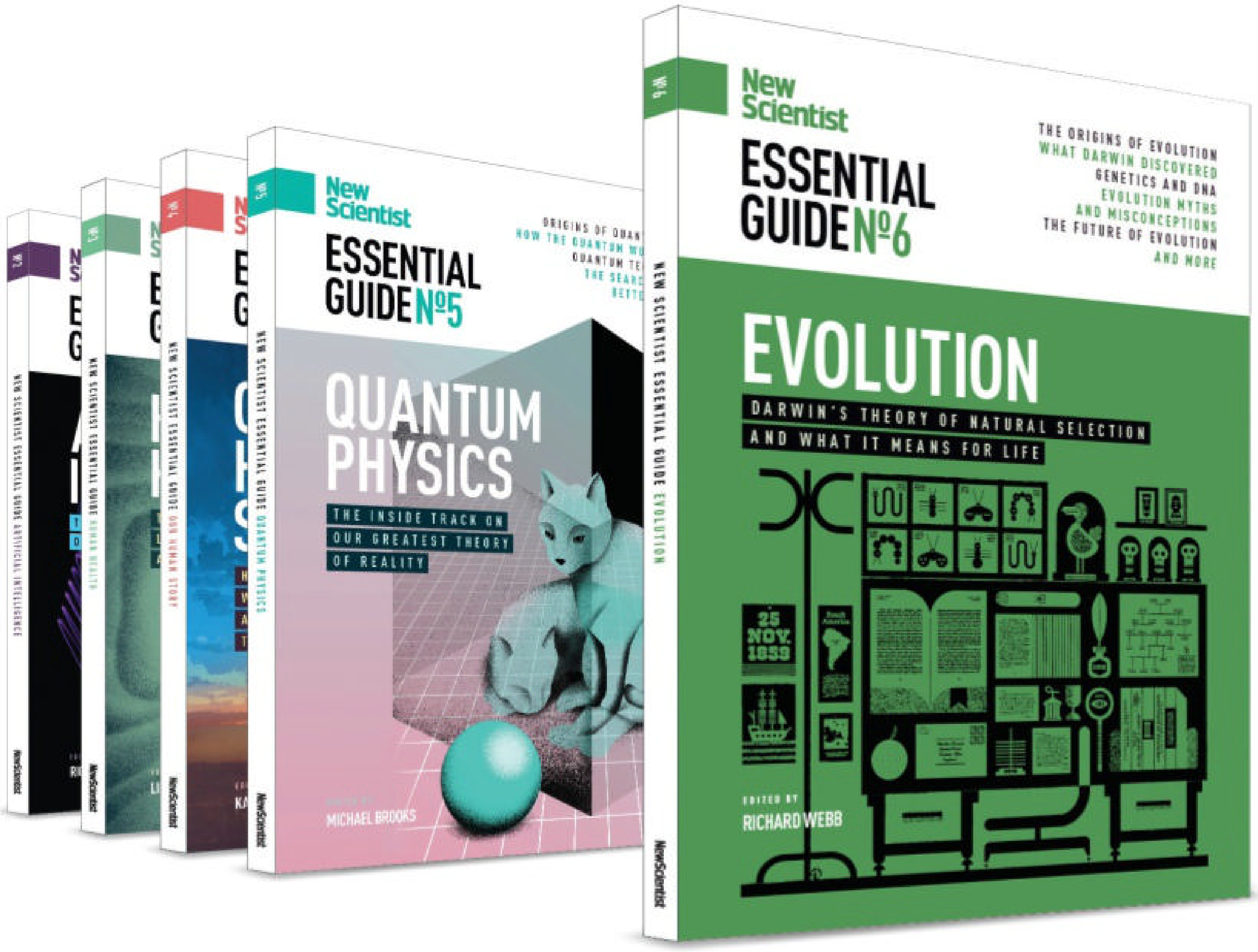
That leads us back to the original question. If evolution is so precocious, why hasn't it created a wheeled animal yet?

Hoyal Cuthill offers a blunt answer. "Wheels are terrible," she says. "The reason so much effort went into the development of the tank is that wheels are atrocious." Sure, they're fine on smooth roads but not so much on badly maintained ones. And in nature, smooth, flat surfaces are rare, so there is no reason for evolution to favour wheels.

The other issue is whether creating a wheel that freely rotates about an axle is beyond evolution, says Vermeij. It is hard to imagine how the wheel might receive nutrients from the rest of the body, as any blood vessels would be torn away. "The wheel might be one of the very few things that may just not be accessible to living things, other than by making a machine as we have done," says Vermeij.

Yet he points out that even if wheels and axles aren't possible, organisms have still found ways to travel using rotational motion. "There are spiders that manage to actively roll down a hill by using their limbs to propel themselves as they form a ball," he says.

Hoyal Cuthill has a final suggestion. "A ball can move rotationally with more degrees of freedom, in more directions, than a wheel on an axle," she says. "Wheels are prone to getting stuck or falling over," she says; balls don't have that problem. So evolution might not have made wheeled creatures simply because it has other solutions. That's just how natural selection rolls. ▮



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CHAPTER 5

EVOLUTION'S OPEN QUESTIONS

As powerful as evolution is as a framework for interpreting the natural world, we are far from having a complete understanding.

In this chapter, we look at some very live questions changing our understanding of the theory – from the basic puzzle of what a species is, to new questions about how genes and the environment interact to effect evolutionary change.

Species are the basic unit of accounting in the natural world, and a central concept in evolution. Yet the theory's central message is that species morph into other species – so can there even be a clean definition of what constitutes a species?

WHAT IS A SPECIES?

"IT IS really laughable to see what different ideas are prominent in various naturalists' minds, when they speak of 'species'... It all comes, I believe, from trying to define the undefinable."

Strong stuff – and from a surprising source. Charles Darwin wrote those lines in a letter to fellow naturalist Joseph Hooker, just three years before the publication of *On the Origin of Species*. Darwin clearly had a problem with the word to which his name is now so intimately linked. It turns out he is not alone. Today, some 160 years after he revolutionised biology, how to define a species is more problematic than ever.

You probably learned that a species is a group of individuals that can breed to produce fertile offspring, but this is just one of dozens of competing definitions. The lack of consensus on what a species is has big implications for how we think about the natural world, for our efforts to conserve it – and even how we think of ourselves as humans.

The idea that the living world is divided into distinct species has deep roots. Frank Zachos at the Natural History Museum Vienna, Austria, suspects it predates the written word. He thinks that even livestock farmers living 10,000 years ago understood it. "Cows produce cows," he says. "Dogs produce dogs." Early farmers would have noticed this and seen it as reflecting some underlying order to the natural world.

For much of human history, people credited the

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PREVIOUS PAGE: KHALUS/ISTOCK
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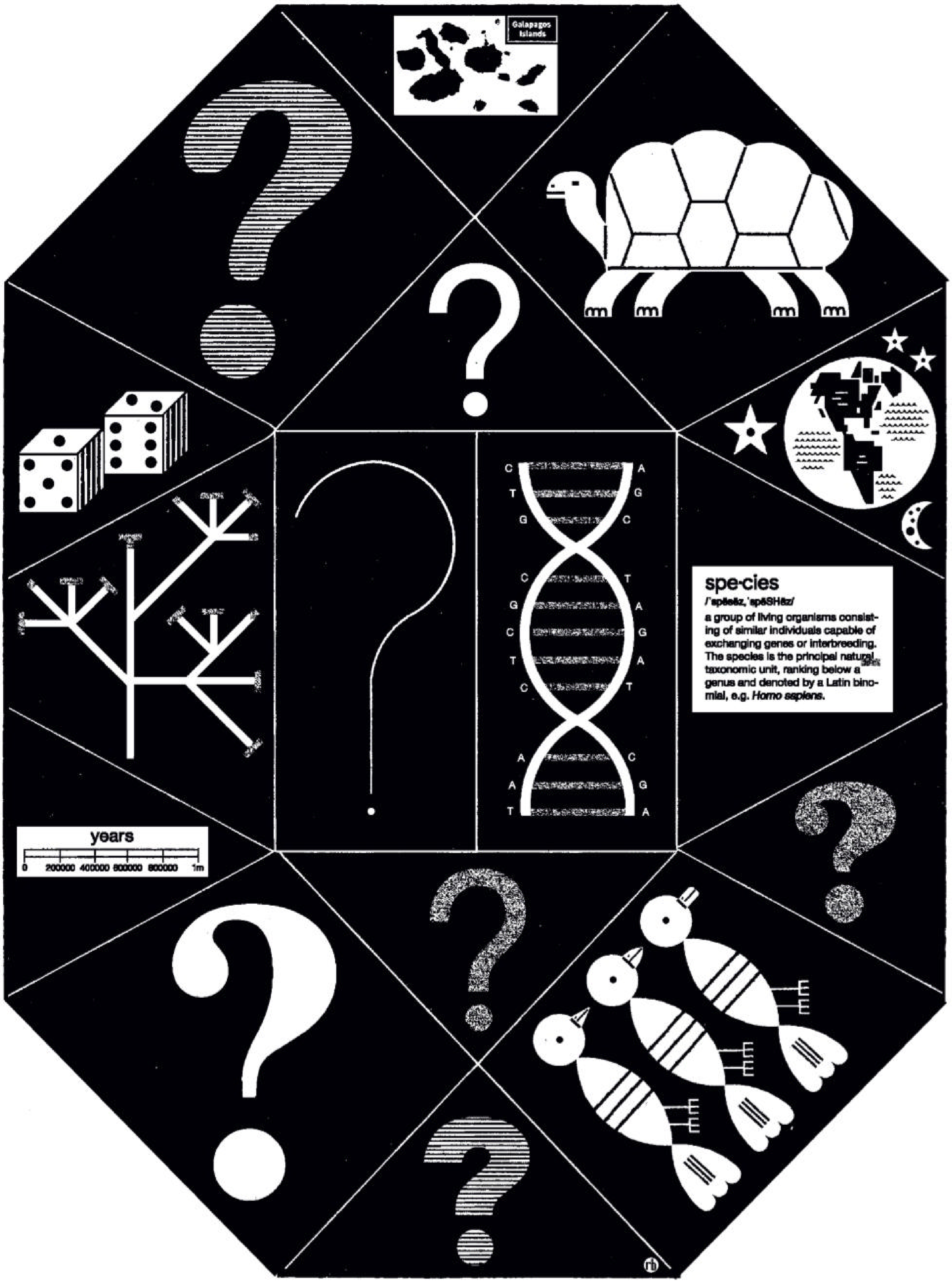

spe·cies

/ˈspēsēz, ˈspēSHēz/

a group of living organisms consisting of similar individuals capable of exchanging genes or interbreeding. The species is the principal natural taxonomic unit, ranking below a genus and denoted by a Latin binomial, e.g. *Homo sapiens*.

gods for that order; species were created at the dawn of time and remained fixed and unchanging. It was this belief that Darwin undermined in the 1850s. But even before him, biologists were having problems with the idea that species never change. In the 18th century, for example, Carl Linnaeus, the "father of taxonomy", was disturbed by a specimen of common toadflax that had a mutant flower. He likened it to a calf born with a wolf's head. Perhaps sometimes a cow does produce a dog after all.

Linnaeus eventually conceded that species created by God could occasionally cross with each other to generate new forms – hybrids. But for Darwin, that was an unsatisfactory solution. Nature may seem to comprise distinct species – killer whales, koalas, capybaras, Galapagos tortoises, blue-footed boobies, and all the rest – but his research emphasised that organisms form populations, and that these populations sometimes fragment, evolving into separate entities, or lineages. Species, he believed, are these lineages. "That was arguably the most original thing about his work," says Brent Mishler at the University of California, Berkeley. "Lineages diverge and at some point, for convenience, we call them different species. But nothing magical has happened at that point." In other words, Darwin considered it arbitrary to choose a single point in the gradual evolution of a distinct form and claim a new species has appeared.

Darwin recognised that his ideas posed a profound problem for the way biologists define species. Curiously, though, his work didn't lead to a reappraisal of the concept. Rather, the "modern synthesis" of evolutionary biology, which pulled together Darwin's work on evolution and Gregor Mendel's on heredity, saw species as a real and distinct level of biological organisation, as valid as the molecule, cell or organism. The synthesis was so influential that it still shapes the way many of us think of species. It is why we tend not to see them as arbitrary. And it explains the popularity of the biological species concept. "That made it into the textbooks," says Zachos. And from there into the popular imagination.

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Turn back to chapter 3 for more on the "modern synthesis"

Behind the scenes, however, a different story was playing out. In the past century, scientists have redefined what a species is time and again, heaping confusion upon confusion (see "Six ways to define a species", right). Zachos identifies no fewer than 32 competing definitions in his 2016 book on the subject, *Species Concepts in Biology*, and notes that two more have been added since then. This partly reflects the distinct ways that researchers in different subsets of biological science see the living world. Ecologists, for example, focus on environment, resources and adaptations, whereas palaeontologists are more interested in the shape of the fossils they study. It also reflects developments in science, with advances in genetics now making it possible to decode the DNA of individual organisms and reconstruct family trees. The upshot is often acrimonious, with players championing their favoured species concept while simultaneously taking pot-shots at rival ideas.

The profusion of definitions also causes practical problems because different types of biologists use different species concepts. Put simply, an insect species might not be equivalent to a mammal species or a flower species – even though most of us assume they are. "A lot of research is based on counting species," says Zachos. "It's as if we think we're all using US dollars, but in reality we're lumping together Japanese yen, euros, US dollars and pounds."

These problems are exposed whenever researchers change their definition of species – something that is happening increasingly often. For instance, in 2011, some biologists studying hoofed mammals shifted from a biological species concept approach to one based on heritable differences. Instantly, the number of species in the group rose from 143 to 279. Zachos and others worry about the consequences of such "taxonomic inflation" for conservation. Inflation, he points out, is often associated with a devaluation of the currency. Society might care a little less about

SIX WAYS TO DEFINE A SPECIES

If you think you know what a species is, think again. There are 34 competing definitions, including the six below.

BIOLOGICAL SPECIES CONCEPT

A species is a population of individuals that can reproduce to generate fertile offspring, and that is reproductively isolated from other populations.

GENETIC SPECIES CONCEPT

A species is a population of individuals that can reproduce and has a distinct genetic profile. Occasional interbreeding with other populations can occur if it doesn't compromise the species' genetic fingerprint.

MORPHOLOGICAL SPECIES CONCEPT

A species is a group of organisms whose physical features are consistently and persistently distinct from those of other groups.

ECOLOGICAL SPECIES CONCEPT

A species is a set of organisms adapted to a particular niche, whose distinct behaviours and morphology result from that adaptation.

RECOGNITION SPECIES CONCEPT

A species is a group of organisms that recognise each other as potential mates.

UNIFIED SPECIES CONCEPT

All separately evolving branches in an evolutionary tree are individual species.

losing a few species to extinction.

Worse still, as biologists change the way they define species, conservation efforts can come in for criticism. This happened in 2018 when a team used DNA studies to conclude that the Chinese giant salamander fell into five distinct "species-level" groups, where just one had previously been recognised. The critically endangered salamanders are bred in farms and some are released back into the wild to boost population numbers. What is now clear is that if their parents are from different species, these offspring will be hybrids. Releasing them risks destroying the fragile genetic distinctions between the five species, and sending some of them extinct. The researchers called the conservation management approach "well-intentioned, but misguided". One argued that we should now focus on identifying and saving the few remaining "unhybridised" salamanders.

The International Union for Conservation of Nature's Red List of Threatened Species recognises that species integrity is an issue in conservation. But its head, Craig Hilton-Taylor, feels that biologists need to rethink their attitudes towards hybrids. He cites the example of the northern white rhino, which is now down to just two individuals, both female. We can either accept that the species is effectively extinct or try to breed them with southern white rhinos. "You'll have a hybrid – but you'll save some of those genes from the northern white rhino," he says. That may be a compromise too far for some, because the general attitude is that hybrids are in some way unnatural and of lower intrinsic value. But this view is outdated. It arises from the assumption that species, at least in the animal kingdom, are distinct once formed. In the past few decades, however, biologists have been astonished to discover that the opposite is true: hybridisation between animal species is common. Genetic analysis reveals, for example, that the critically endangered red wolf is a cross between the grey wolf and coyote. Likewise, one of the world's rarest fish, the Devil's Hole pupfish, seems to be a hybrid.

The hybrid issue extends all the way to our doorstep. Today, most of us are familiar with the discovery that there is Neanderthal or Denisovan DNA in the cells ›

“Experts in human evolution are cautious about using the term ‘species’ ”

of many living humans. If we consider these other hominins to be distinct species, then that would make many of us “unnatural” or “valueless” hybrids, which is absurd. But the fact that such a conclusion could be reached might help explain why some experts in human evolution are cautious about using the term “species”. These include geneticist Johannes Krause of the Max Planck Institute for the Science of Human History in Jena, Germany, who with his colleagues first identified the Denisovans. They didn’t – and still haven’t – claimed Denisovans to be a distinct species. They prefer the less loaded term “population”.

Language matters. Reporting one of the most astonishing science news stories of 2018, the cover of *Nature* read: “Ancient Human Hybrid”. It referred to research by Krause’s colleagues, who discovered that an ancient human, dubbed Denny, had a Neanderthal mother and a Denisovan father. “The research paper is so careful not to use the word hybrid,” says John Hawks at the University of Wisconsin-Madison. “And yet it is there on the cover of the journal: hybrid found!” He points out that the genetic difference between Denny’s father and mother may reflect a history of divergence that lasted no longer than that seen between some human populations that happily intermix today. “But it would be wrong to look at a living person and say: hybrid,” he says. “We don’t use that term for a reason.”

Given that the species concept is so divisive and so nebulous, what is to be done? One step might be to bring more rigour to the process of recognising new species. Stephen Garnett at Charles Darwin University, Australia, thinks that the ease with which new species are now recognised has led to “taxonomic anarchy”. In 2017, he and Les Christidis at Southern Cross University, Australia, argued that a formal process should be set up to judge the merit of any putative new species before it is officially adopted. “It gives the process legitimacy,” says Garnett. Immediate reaction to the proposal was negative, he admits, but he has since found common ground with some critics. “They do realise there is an issue that needs dealing with,” he says.

This could aid conservationists struggling with taxonomic inflation. It might also help focus thinking about our own ancestors when we come to classify new hominin fossils and ancient “ghost” populations – mysterious ancestors currently known only from the distinct traces they have left in our DNA. But it still leaves the problem that we have multiple definitions of what constitutes a species. One way to solve this might be to go back to Darwin and his emphasis on species as lineages, which is actually a common feature of most of the competing species concepts, according to Kevin de Queiroz at the Smithsonian Institution in Washington DC. De Queiroz’s “unified species concept” recognises that the moment a population fragments, the lineage that arises becomes another species. At this early stage, its members might lack distinct genetic and physical features, but, gradually, they begin to diverge in such ways. Every time the species gains another distinct feature, such as reproductive isolation, it becomes easier for us to recognise it as something different. Yet it has been a species from the very start, he argues.

Problem solved? Not even close, according to some. Zachos points out that we must still make an arbitrary choice about which populations are species and which are not, unless we want to name every one of them a

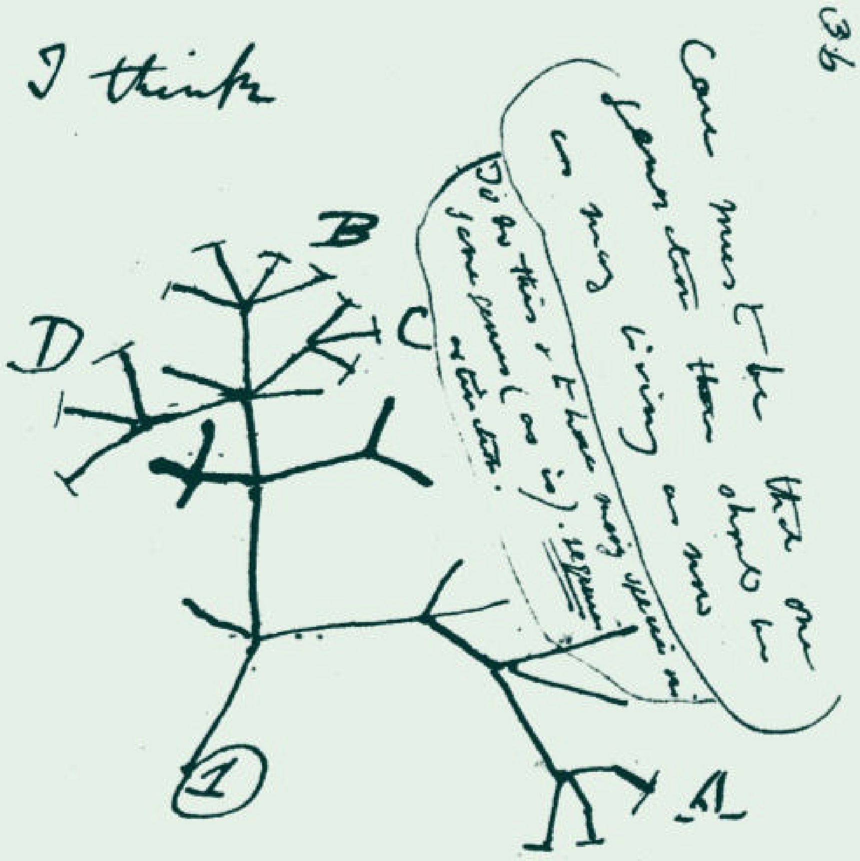
Would hybridisation save the northern white rhino as a species?

REUTERS/ALAMY STOCK PHOTO

species. That would be socially unacceptable if it ever led to different living human populations being recognised as distinct species. Besides, we would need a crystal ball to see whether fragmenting populations will remain truly separated or whether it is just a blip before they come back together again.

Perhaps, instead, the ultimate solution is simply to remove the word "species" from the scientific lexicon. In 2018, Mishler and John Wilkins at the University of Melbourne, Australia, set out this argument. They suggested that we should focus on another division of life, the "clade", a group sharing a common ancestor and so comprising a separate twig on the tree of life. They say we could classify organisms as the Smallest Named and Registered Clade, or SNaRC, rather than as species. So, for example, Neanderthals, Denisovans and living humans would be three distinct SNaRCs. There is nothing intrinsically special about SNaRCs, according to Mishler: they might interbreed or not, and the groups that fit the classification would vary across the tree of life, forcing us to accept that there is no common currency. By abandoning "species" and turning to "SNaRCs", he argues, biologists would have a blank slate for thinking about biodiversity.

Needless to say, the idea has critics. "Darwin's book was on the origin of species, and that's because species are a real problem," says Hawks. "To say 'Oh, we're not going to deal with species anymore' – it's actually a cop out." But Zachos reluctantly concedes that Mishler's idea might be part of a lasting solution to the species problem. "If I could think of something that would prove his thinking is wrong, I'd be a happy man," he says. "So far I can't." ▮


I think
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Case must be that one generation then should be as many living as now
To do this & to have many species in same genus (as is) requires extinction.
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WHERE DO WE GET OUR GENES FROM?

The work of Mendel and the geneticists who followed him showed that genes passed by parents to their offspring are the main mechanism by which traits are inherited. But more recently we've realised it isn't the only one.

IN JULY 1837, Charles Darwin had a flash of inspiration. In his study at his house in London, he turned to a new page in his red leather notebook and wrote, "I think". Then he drew a spindly sketch of a tree (shown above).

As far as we know, this was the first time Darwin toyed with the concept of a "tree of life" to explain the evolutionary relationships between different species. It was to prove a fruitful idea: by the time he published *On the Origin of Species* 22 years later, Darwin's spindly tree had grown into a mighty oak. The book contains numerous references to the tree and its only diagram is of a branching structure showing how one species can evolve into many.

The tree-of-life concept was absolutely central to Darwin's thinking, equal in importance to natural selection, according to biologist W. Ford Doolittle at Dalhousie University in Halifax, Nova Scotia, Canada. Without it, the theory of evolution would never have happened. The tree also helped carry the day for evolution. Darwin argued successfully that the tree of life was a fact of nature, plain for all to see though in need of explanation. The explanation he came up with was evolution by natural selection.

Ever since Darwin the tree has been the unifying principle for understanding the history of life on Earth. At its base is LUCA, the Last Universal Common Ancestor of all living things, and out of LUCA grows a trunk, which splits again and again to create a vast, bifurcating tree.

Each branch represents a single species; branching points are where one species becomes two. Most branches eventually come to a dead end as species go extinct, but some reach right to the top – these are living species. The tree is thus a record of how every species that ever lived is related to all others right back to the origin of life.

For much of the past 150 years, biology has largely concerned itself with filling in the details of the tree. "For a long time the holy grail was to build a tree of life," says Eric Bapteste, an evolutionary biologist at the Pierre and Marie Curie University in Paris, France. But many biologists now argue that the tree concept is obsolete and needs to be discarded. "We have no evidence at all that the tree of life is a reality," says Bapteste.

So what happened? In a nutshell, DNA. The discovery of the structure of DNA in 1953 opened up new vistas for evolutionary biology. Here, at last, was the very stuff of inheritance into which was surely written the history of life, if only we knew how to decode it. Thus was born the field of molecular evolution, and as techniques became available to read DNA sequences and those of other biomolecules such as RNA and proteins, its pioneers came to believe that it would provide proof positive of Darwin's tree of life. The basic idea was simple: the more closely related two species are (or the more recently their branches on the tree split), the more alike their DNA, RNA and protein sequences ought to be.

It started well. The first molecules to be sequenced were RNAs found in ribosomes, the cell's protein-making machines. In the 1970s, by comparing RNA sequences from various plants, animals and microorganisms, molecular biologists began to sketch the outlines of a tree. This led to, among other successes, the unexpected discovery of a previously unknown major branch of the tree of life, the unicellular archaea, which were previously thought to be bacteria.

By the mid-1980s, there was great optimism that molecular techniques would finally reveal the universal tree of life in all its glory. Ironically, the opposite happened.

The problems began in the early 1990s when it became possible to sequence actual bacterial and archaeal genes rather than just RNA. Everybody expected these DNA sequences to confirm the RNA tree, and sometimes they did but, crucially, sometimes they did not. RNA, for example, might suggest that species A was more closely related to species B than species C, but a tree made from DNA would suggest the reverse.

Which was correct? Paradoxically, both – but only if the main premise underpinning Darwin's tree was incorrect. Darwin assumed that descent was exclusively "vertical", with organisms passing traits down to their offspring. But what if species also routinely swapped genetic material with other species, or hybridised with them? Then that neat branching pattern would quickly degenerate into an impenetrable thicket of interrelatedness, with species being closely related in some respects but not others.

We now know that this is exactly what happens. As more and more genes were sequenced, it became clear that the patterns of relatedness could only be explained if bacteria and archaea were routinely swapping genetic material with other species – often across huge taxonomic distances – in a process called horizontal gene transfer (HGT).

At first HGT was assumed to be a minor player, transferring only "optional extra" functions such as antibiotic resistance. Core biological functions such as DNA replication and protein synthesis were still thought to be passed on vertically. For a while, this allowed evolutionary biologists to accept HGT without jeopardising their precious tree of life; HGT was merely noise blurring its edges. We now know that view is wrong. "There's promiscuous exchange of genetic information across diverse groups," says Michael Rose, an evolutionary biologist at the University of California, Irvine.

As it became clear that HGT was a major factor, biologists started to realise the implications for the tree concept. As early as 1993, some were proposing that for bacteria and archaea the tree of life was more like a web. In 1999, Doolittle made the provocative claim that "the history of life cannot properly be represented as a tree". "The tree of life is not something that exists in ›

ART COLLECTION/ALAMY STOCK PHOTO

nature, it's a way that humans classify nature," he says.

HGT has been most frequently documented in bacteria and archaea. These organisms are prokaryotes, single-celled microbes that lack a nucleus and so have few physical barriers to stop DNA from elsewhere being incorporated into their genome. But in the past couple of decades, it's become clear it also occurs among eukaryotes, organisms encompassing everything from fungi to humans whose DNA is tucked away within a cell nucleus.

For a start, it is increasingly accepted that the eukaryotes originated by the fusion of two prokaryotes, one bacterial and the other archaeal, forming this part of the tree into a ring rather than a branch.

The neat picture of a branching tree is further blurred by a process called endosymbiosis. Early on in their evolution, eukaryotes are thought to have engulfed two free-living prokaryotes. One of these gave rise to the cellular power generators called mitochondria while the other was the precursor of the chloroplasts, in which photosynthesis takes place.

These "endosymbionts" later transferred large chunks of their genomes into those of their eukaryote hosts, creating hybrid genomes. As if that weren't complicated enough, some early eukaryotic lineages apparently swallowed one another and amalgamated their genomes, creating yet another layer of horizontal transfer.

This genetic free-for-all continues to this day. The vast majority of eukaryote species are unicellular – amoebas, algae and the rest of what used to be known as "protists". These microscopic beasties have lifestyles that resemble prokaryotes and, according to Jan Andersson at the University ofUppsala in Sweden, their rates of HGT are often comparable to those in bacteria.

More fundamentally, recent research suggests that the evolution of animals and plants isn't exactly tree-like either. For example, hybridisation clearly plays an important role in the evolution of plants. According to Loren Rieseberg, a botanist at the University of British Columbia in Vancouver, Canada, around 14 per cent of living plant species are the product of the fusion of two separate lineages.

Some researchers are also convinced that hybridisation has been a major driving force in animal evolution, and that the process is ongoing. "It is really common," says James Mallet, an evolutionary biologist at University College London. "Ten per cent of all animals regularly hybridise with other species." This is especially true in rapidly evolving lineages with lots of recently diverged species – including our own. There is evidence that early modern humans hybridised with our extinct relatives, such as *Homo erectus* and the Neanderthals.

It is becoming increasingly apparent that HGT plays an unexpectedly big role in animals too. As ever more multicellular genomes are sequenced, ever more incongruous bits of DNA are turning up. Back in 2007, for example, a team at the University of Texas at Arlington found a peculiar chunk of DNA in the genomes of eight animals – the mouse, rat, bushbaby, little brown bat, tenrec, opossum, anole lizard and African clawed frog – but not in 25 others, including humans, elephants, chickens and fish. This patchy distribution suggests that the sequence must have entered each genome independently by horizontal transfer.

Other cases of HGT in multicellular organisms are coming in thick and fast. HGT has been documented in insects, fish and plants, and a few years ago a piece of snake DNA was found in cows. The most likely agents of this genetic shuffling are viruses, which constantly cut and paste DNA from one genome into another, often across great taxonomic distances.

In fact, by some reckonings, 40 to 50 per cent of the human genome consists of DNA imported horizontally by viruses, some of which has taken on vital biological functions. The same is probably true of the genomes of other big animals. "The number of horizontal transfers in animals is not as high as in microbes, but it can be evolutionarily significant," says Bapteste.

Nobody is arguing – yet – that the tree concept has outlived its usefulness in animals and plants. While vertical descent is no longer the only game in town, it is still the best way of explaining how multicellular organisms are related to one another. Darwin's vision of a tree of life wasn't wrong – it's just a more tangled thicket than we've come to believe. ▮

ARE GENES REALLY DESTINY?

The more we learn about our genetics, the clearer it is becoming that "genetic determinism" must be added to our list of evolutionary myths. A given set of genes doesn't set an organism's characteristics in stone. Factors such as junk DNA and "epigenetic" effects mean it is just a loose template that can produce a variety of observable characteristics depending on the environment and other factors.

AT THE dawn of the new millennium, two rival teams were vying to be the first to sequence the human genome. Their findings, published in February 2001, made headlines around the world. Back-of-the-envelope calculations had suggested that to account for the sheer complexity of human biology, our genome should contain roughly 100,000 genes.

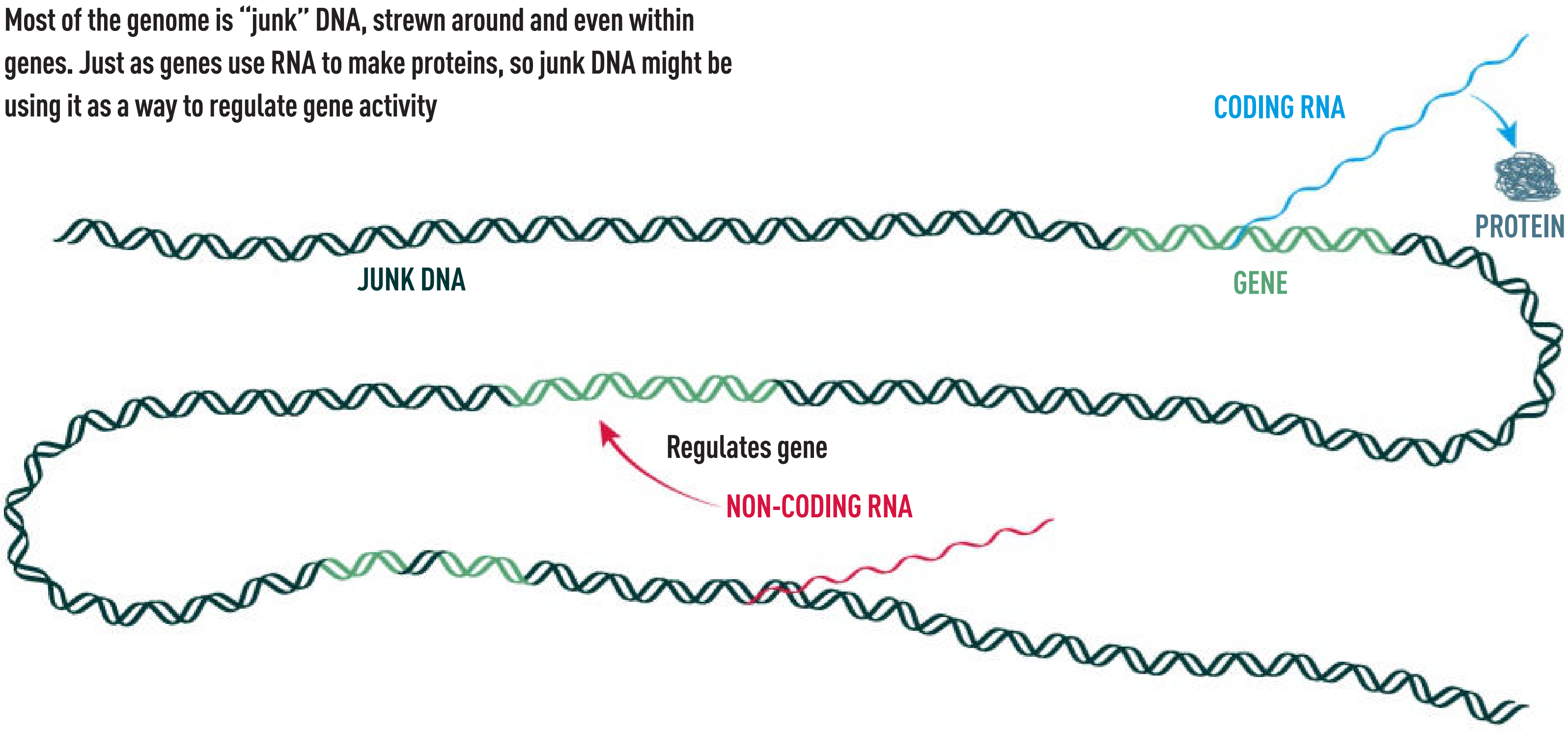
The estimate was wildly off. Both groups put the actual figure at around 30,000. We now think it is even fewer – just 20,000 or so. "It was a massive shock," says geneticist John Mattick. "That number is tiny. It's effectively the same as a microscopic worm that has just 1000 cells."

The implication is that the blueprint for building a human, or indeed any complex creature, lies not only in our genes but in other, neglected parts of our genome. This long-overlooked DNA could have shaped iconic traits such as our upright stance, opposable thumbs, big brains, capacity for language, even our tendency to form monogamous relationships. We might like to think of ourselves as pinnacles of evolution, but actually we are mostly made of junk.

We now know that genes – the sequences of DNA that code for proteins – account for just 1 or 2 per cent of our genome. For a long time the rest was considered to have no function at all, earning it the dismissive title "junk DNA". But it's now clear that this trash hides treasure – bits of DNA that control genes like a conductor directing an orchestra, switching them on and off at different times and in different cells.

These discoveries have come from studies ›

Most of the genome is "junk" DNA, strewn around and even within genes. Just as genes use RNA to make proteins, so junk DNA might be using it as a way to regulate gene activity



comparing the human genome, junk and all, with those of chimps, mice and other animals. Some have even compared the genomes of Neanderthals and other extinct human species. The aim is to identify bits that look suspiciously different in modern humans, regions that are uniquely ours.

James Noonan at Yale University and Shyam Prabhakar at the Genome Institute of Singapore did this comparison across all mammals. They homed in on one piece of supposedly junk DNA called *HACNS1*, which has accumulated an unusually large number of mutations since humans split from chimps. Inserting it into the genomes of mouse embryos, along with a tiny, molecular label that would change colour whenever it was modifying the activity of surrounding genes, they found the label popped up in the embryos' paws, in the area where digit 1 forms. In humans, that is either the thumb or big toe, suggesting that *HACNS1* might influence their development.

For an idea of how, we can look at the fossil record. "Human thumbs and feet are among the most distinctive features of our species," says Prabhakar. There is evidence that our ancestors evolved opposable thumbs about 3 million years ago, roughly when they began to use stone tools and only a few million years after we split from chimpanzees. It's likely that early humans were also standing upright and were starting to walk on two legs around the same time or a little earlier. Doing so was tied to physical changes: toes shrank and foot arches became more rigid.

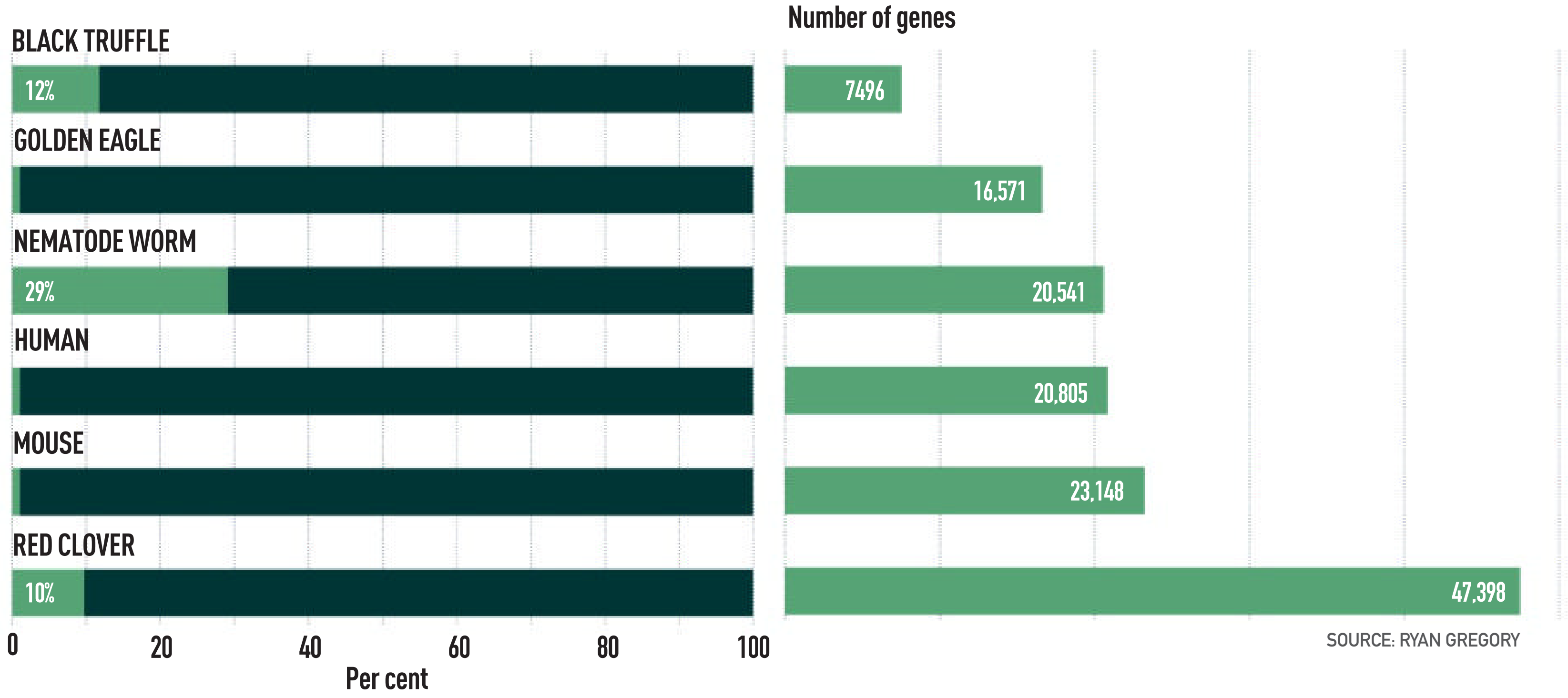
According to Prabhakar and Noonan, all this could have been happening around the time that *HACNS1* began altering gene activity in our hands and feet. By subtly changing when and where genes were switched on, this little piece of DNA could have been modifying our hands and feet.

The study is not the only one to suggest that genetic controllers, rather than genes themselves, played a crucial part in shaping us. Gene activity is often regulated via methylation, a process in which a chemical unit called a methyl group is attached to a gene segment, influencing how much protein it produces. In 2013, a study suggested that DNA methylation had helped our transition to walking on two legs, and perhaps our language skills too. Andrew Sharp of the Icahn School of Medicine at Mount Sinai, New York, and his colleagues compared DNA methylation patterns in humans, chimps, gorillas and orangutans, and found 171 genes with uniquely human patterns. A closer look suggested that these genes were involved in a handful of traits: regulating blood pressure, controlling the development of the inner ear and shaping facial muscles.

"What are the big differences between humans and chimps? We walk upright and we speak," says Sharp. Walking upright lifted the brain, which meant our ancestors had to change how they regulated blood pressure to keep the brain supplied with enough oxygen. It also demanded exceptional balance, typically improved by modifying the inner ear.

Humans are not remarkable either in the number of genes we have or in the proportion of genes in our genome. So is junk DNA what makes us human?

PROPORTION OF GENES TO JUNK



SOURCE: RYAN GREGORY

Speech, meanwhile, required an unprecedented level of control over the muscles in our face and around our mouth. Similar studies reconstructing Neanderthal methylation patterns and comparing them with human ones have also found key differences in genes that control limb development, suggesting methylation could have contributed to giving us longer legs than our extinct cousins.

Mattick, who is at the Garvan Institute of Medical Research in Sydney, Australia, thinks that junk DNA controls methylation. He suggests cells might transcribe junk into RNA, molecules typically associated with the process of making proteins (see diagram). But this "non-coding" RNA does something else: it influences when and where DNA methylation occurs. Think of the genome as a set of organic building blocks. The proteins that genes code for are generic components that can be used to construct almost any animal. Encoded in our junk DNA, meanwhile, is a set of instructions for how to assemble them to make one species or another.

Methylation alters how genes are expressed without altering the underlying DNA sequence. What makes it a powerful evolutionary force is that it provides a way to create heritable changes in an organism's phenotype – its observable traits. Such evolutionary change in the absence of genetic change is known as epigenetics.

Some of the best evidence for epigenetics comes from a dark episode in human history. In late 1944, as retaliation for a Dutch rebellion against German occupiers, the Nazis cut off food and fuel supplies to the Netherlands. By the time the country was liberated, adults were subsisting on an average of 580 calories per day. Children born to women who were pregnant during this time were small and had low birth weights. Surprisingly, though, later in life they had unusually high levels of obesity, diabetes and schizophrenia. So, too, did their children.

Within the conventional view, hardwired, genes-based view of evolution, the effects of the environmental shock of the Dutch "hunger winter" should not have been passed between generations. But it does make sense if epigenetic marks, such as methylation, are being passed down. The marks can be created in response to changes in conditions within cells or the external environment, such as including temperature, stress or diet. Marks created when food was scarce might become associated with a high incidence of metabolic diseases in times of plenty.

Subsequent studies in plants and animals suggest that epigenetic inheritance is more common than anyone had expected. What's more, compared with genetic inheritance, it has some big advantages. Environments can change rapidly and dramatically, but genetic mutations are random, so often require generations to take hold. Epigenetic marks, by contrast, are created in minutes or hours. And because they result from environmental change, they are often adaptive, boosting the survival of subsequent generations.

Take the pea aphid. It is capable of both sexual and › asexual reproduction, and comes in two varieties: winged and wingless. When scientists exposed a group of genetically identical pea aphids to ladybirds, the proportion of winged aphids increased from a quarter to a half. This adaptation, which helped them escape the predatory ladybirds, persisted for 25 generations. The aphid DNA didn't mutate, the only change was epigenetic.

Epigenetic bequests aren't always beneficial. Experimenting with nematode worms, Martin Lind at Uppsala University in Sweden and his colleagues have discovered that the key factor is whether environmental conditions remain stable. If they change, then adaptations may be detrimental to subsequent generations – as happened with descendants of the Dutch hunger winter.

The extent of epigenetic inheritance is contested. Some sceptics point out that, during mammalian reproduction, the creation of sperm and egg cells involves erasing epigenetic markers. Others argue that epigenetic transmission across generations is extremely widespread and useful. In plants, for example, it can account for differences in fruit size, flowering time and many other survival-boosting traits.

There is no doubt, however, that a given set of genes, or genotype, can produce very different phenotypes depending on environmental conditions. An Arctic fox changes its coat colour with the seasons. The presence of predators causes water flea *Daphnia longicephala* to grow a protective helmet and spines. Even a change in social environment can prompt a shift. In the European paper wasp (*Polistes dominula*), for example, when the queen dies, the oldest worker transforms herself into a new queen. But she isn't the only one to respond. Seirian Sumner at University College London and her colleagues found that the death of a colony's queen results in temporary changes in the expression of genes in all workers, as though they are jostling genetically for succession. This flexibility is key to the survival of the colony and the species, says Sumner.

The power of "genetic plasticity" can be seen in the humble house finch. In the past 50 years, it has colonised the eastern half of North America, moving into habitats ranging from pine forests near the Canadian border to swampland in the Gulf of Mexico. The finch's underlying developmental plasticity provided the raw material from which novel features evolved, including a range of new colourings and other physical and behavioural traits, says David Pfennig at the University of North Carolina at Chapel Hill. "Stop thinking about this as being like genes or environment, because it's a combination of the two," he says.

One consequence is that some of the evolutionary ideas championed by the French biologist Jean-Baptiste Lamarck before Darwin developed his theory of evolution by natural selection might not be so wide of the mark after all. He had argued that traits themselves could be handed down from generation to generation, and this was a mechanism by which novel traits could evolve – the giraffe's long neck, for instance, arising as the result of successive generations of animals reaching to higher branches for food.

←
See chapter 1 for more on the history of evolutionary ideas

The Mexican spadefoot toad (*Spea multiplicata*) might show a sort of plasticity-led, or "neo-Lamarckian" evolution. It breeds in ponds that appear after summer monsoons and the newly hatched tadpoles typically survive on a diet of algae and bacteria. However, should tadpoles find themselves in a pond where fairy shrimps are available, they adapt to take advantage of the more nutritious fare, developing larger jaws and shorter guts. To Nicholas Levis at the University of North Carolina at Chapel Hill, spadefoot toads provide a perfect example of plasticity-led evolution. "It reorients how we think about the adaptive process," he says.

Such plastic changes occur because an environmental trigger affects an organism's development in some way. Levis has found that in the spadefoot toads this happens via 14 genes that underpin their ability to switch between the two different body types. If the environment remains unchanged – abundant shrimps in the case of the tadpoles – then subsequent generations will continue to exhibit the traits that help them survive. But these traits are induced anew each time by the environment, not directly inherited from a parent, so how can they affect evolution?

Plasticity may buy organisms valuable time to adapt genetically. Here's how it might work. In an environment where survival depends on a particular response, only mutations that reinforce that response, or at least don't undermine it, will spread so that eventually a plastic change becomes "fixed".

We don't know how prevalent this sort of evolution is, but one study found that if you put fish on land they learn to "walk". Admittedly, the fish in question were bichir fish, which can breathe air and haul themselves along out of water if necessary. Nevertheless, simply being on land improved their walking abilities, hinting that plasticity-led evolution might underpin some key transitions in the development of life on Earth, such as the evolution of terrestrial animals – not to mention our own evolution. ▮

KHALUS/ISTOCK

CAN EVOLUTION LEARN?

The conventional view of evolutionary change is of natural selection favouring whichever of countless, random, spontaneous genetic mutations happen to be good for survival. That still leaves a puzzle of how natural selection creates so much complexity so fast. A bold new hypothesis says it's because it learns and remembers past solutions, just as our brains do.

A FEATHER isn't just pretty: it's pretty useful. Strong, light and flexible, with tiny barbs to zip each filament to its neighbours, it is fantastically designed for flight. The mammalian eye, too, is a marvel of complex design, with its pupil to regulate the amount of light that enters, a lens to focus it onto the retina, and rods and cones for low light and colour vision – all linked to the brain through the optic nerve. And these are just the tip of the iceberg of evolution's incredible prowess as a designer.

For centuries, the apparent perfection of such designs was taken as self-evident proof of divine creation. Darwin himself expressed amazement that natural selection could produce such variety and complexity. Even today, creationism and intelligent design thrive on intuitive incredulity that an unguided, unconscious process could produce such intricate contraptions. ›

We now know that intuition fails us, with feathers, eyes and all living things the product of an entirely natural process. But at the same time, current ways of thinking about evolution give a less-than-complete picture of how that works. Any process built purely on random changes has a lot of potential changes to try. So how does natural selection come up with such good solutions to the problem of survival so quickly, given population sizes and the number of generations available?

The traditional answer is through so-called massive parallelism: living things tend to have a lot of offspring, allowing many potential solutions to be tested simultaneously. But just recently, some researchers have begun to suggest a radical new addition to the theory of evolution: that, added together, its simple processes of genetic variation, selection and inheritance form an intricate learning machine that draws lessons from past successes to improve future performance.

That's a controversial suggestion at first pass: to invoke learning at all risks violating one of evolution's most important principles. When we learn, we in some way anticipate the future, combining solutions from past experience with knowledge of present conditions to develop a strategy for what we think will come next. But evolution can't see the future: its exploration is born out of random mutations selected or rejected by current circumstances, so it is blind to the challenges to come.

But then again, learning organisms can't actually see the future. When we cross a road, we can't anticipate all traffic movements, but we have a memory bank of solutions that have worked before. We develop a strategy based on those – and if it proves successful, we call on that newly learned experience next time. That's not too dissimilar to what natural selection does when it reuses successful variants from the past, such as the flowers of bee orchids that are unusually good at attracting bees, or the mouthparts of mosquitoes that work like hypodermic syringes and are particularly effective at sucking blood.

Some now think the similarities between learning and evolution go more than skin-deep – and that our understanding of one could help us understand the other. Since the early days of computer science, people have been developing algorithms – iterative rules – that allow computers to combine banked knowledge with fresh information to create new outputs, and so mimic processes involved in learning and intelligence. In recent years, such learning algorithms have come to underlie much technology that we take for granted, from Google searches to credit-scoring systems.

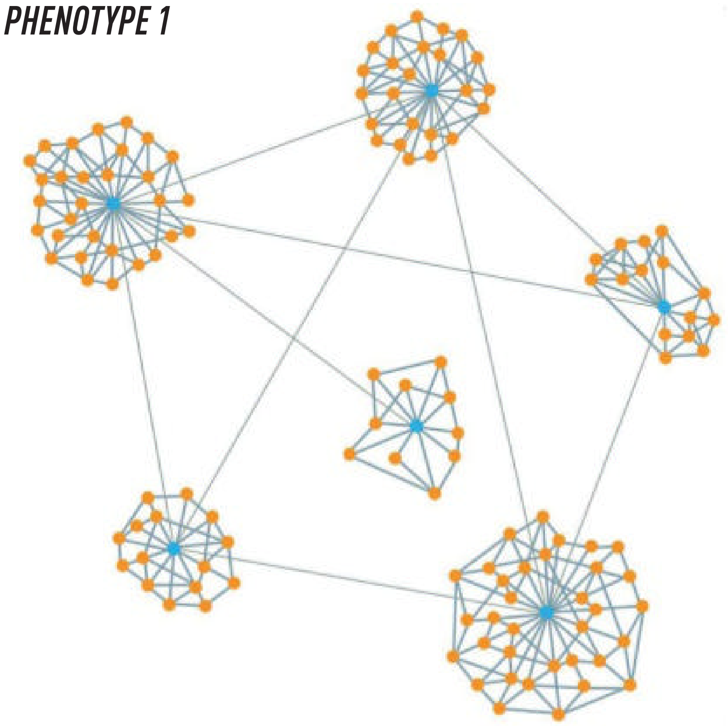
In 2013, Leslie Valiant, a computational theorist at Harvard University, described how the workings of evolution equate to a relatively simple learning algorithm known as Bayesian updating. Used to model everything from celestial mechanics to human decision-making computationally, this type of learning entails starting with many hypotheses and pinpointing the best ones using new information as it becomes available. Replace the hypotheses you want to test with the organisms in a population, Valiant showed, and natural selection amounts to incorporating new information from the surrounding environment to home in on the best-adapted organisms.

In 2014, Erick Chastain at Rutgers University in New Jersey and his colleagues found a similar equivalence between evolution in a sexually reproducing population and another learning model called the multiplicative weights update algorithm. This presumes there may be many potential solutions to a problem, and the key to finding the best lies in weighting their promise based on past performance.

Over time, the genes in an organism evolve to work together in associated groups. The interaction of these clusters determines the organism's characteristics – its phenotype

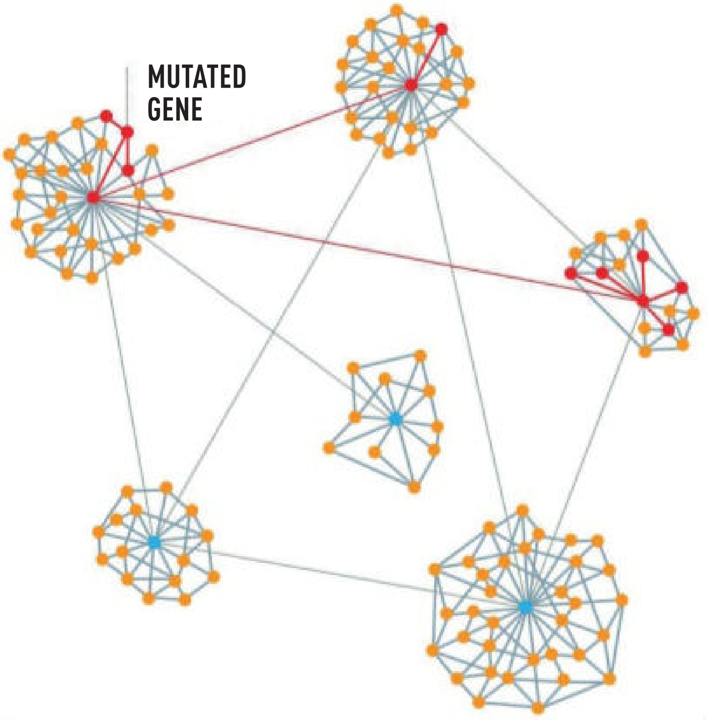
Clumps of associated genes represent "learned' solutions to past evolutionary problems

PHENOTYPE 1



A random mutation to a single gene can change connection strengths across the network, potentially radically changing the phenotype

PHENOTYPE 2



Applying this algorithm and assuming that natural selection gives more weight to previously successful solutions was enough to reproduce how, over generations, evolution homes in on the gene variants with the highest overall evolutionary "fitness".

Such parallels left Richard Watson of the University of Southampton, UK, wondering how a model that more closely follows the genetic changes underpinning evolution might look. Not so long ago, we naively talked about genes "for" particular traits, and assumed for example that humans, being so complex, would have lots of genes. But as we've seen, when in the 1990s two groups were vying to sequence the human genome, they found far fewer gene than they expected. Genes, we now know, are team players: their activity is regulated by other genes, creating a network of connections. The whole is thus capable of much more than the sum of its parts.

These connections mean that mutations, whether caused by spontaneous chemical changes or faulty DNA repair processes, don't just alter single genes. When a mutation changes one gene, the activity of many others in the network can change in concert. The network's organisation is itself a product of past evolution, because natural selection rewards gene associations that increase fitness. This allows your genotype (the set of genes you inherit from your parents) to solve the problem of creating a well-adapted phenotype (the set of outward characteristics that adds up to you). "In evolution, the problem is to produce a phenotype that is fit in a given environment, and the way to do it is to make connections between genes – to learn what goes together," says Watson.

Watson's insight was to realise that this whole process has a lot in common with the workings of one of the cleverest learners we know – the human brain. ›

Our brains consist of neurons connected via synapses. Connections between two neurons are strengthened when they are activated at the same time or by the same stimulus, a phenomenon encapsulated by the phrase "neurons that fire together wire together". When we learn, we alter the strengths of connections, making networks of associations capable of problem-solving.

This is called Hebbian learning after neuropsychologist Donald Hebb, who first described it in the mid-20th century. Simple models based on these networks can do surprisingly clever things, such as recognising and classifying objects, generalising behaviour from examples, and learning to solve optimisation problems. If evolution works in equivalent ways, Watson realised, that could explain why it is such a good problem-solver, creating all that complexity in such short order.

Working with Günter Wagner from Yale University and others, Watson built a model network in which genes can either increase or reduce each other's activity, as they do in nature. They found that simply taking account of genes' networked nature meant that when the genotype had learned solutions, it could remember them and reproduce them in different environments – as indeed our brains can.

Evidence for learning in this sense is often seen in the natural world, for instance in the way a crocodile genome can produce a male or female crocodile depending on the temperature at which the egg is incubated. But learning the way our brains do it is not just about remembering and reproducing past solutions. "A real learning system also has to be able to generalise – to produce good solutions even in new situations it hasn't encountered before," says Watson. Think crossing a road you've never crossed before versus crossing a familiar one.

This generalisation ability rests in recognising similarities between new and old problems, so as to combine the building blocks of past solutions to tackle the problem at hand. But Watson and his colleagues' models show that this kind of learning is also what a gene network does under the pressure of natural selection. The cost associated with making gene connections – proteins must be produced and energy expended – favours networks with fewer connections. Subsets of connections that work well together become bound tightly in blocks that themselves are only loosely associated. Just as our brains do, natural selection memorises partial solutions – and these building blocks are embedded in the structure of the gene network.

This way of working allows genotypes to generate phenotypes that are both complex and flexible. "If past selection has shaped the building blocks well, it can make solving new problems look easy," says Watson. Instead of merely making limbs longer or shorter, for example, evolution can change whether forelimbs and hindlimbs evolve independently or together. A single mutation that changes connections in the network can lengthen all four legs of a giraffe, or allow a bat to increase its wingspan without getting too leggy. And a feather or an eye needn't be generated from scratch, but can evolve by mixing and matching building blocks that have served well in the past (see diagram, page 83).

This ability to learn needs no supernatural intervention – it is an inevitable product of random variation and selection acting on gene networks. "Far from being blind or dumb, evolution is very smart," says Watson. ▮

THE BIGGEST GAPS IN EVOLUTION

To mark the bicentenary of Charles Darwin's birth in 2009, *New Scientist* asked eminent evolutionary biologists to outline the biggest gaps remaining in evolutionary theory. Here's what they said.

RICHARD DAWKINS

EVOLUTIONARY BIOLOGIST, EMERITUS PROFESSOR AT THE UNIVERSITY OF OXFORD, UK

Which facts about evolution had to be true, and which just happen to be true? Did the genetic code have to be digital in order for natural selection to work? Could any other class of molecules have substituted for proteins? How inevitable was the evolution of sex? Eyes? Intelligence? Language? Consciousness? Was the origin of life itself a probable event, and therefore is life common in the universe?

FRANS DE WAAL

PRIMATE ETHOLOGIST AT EMORY UNIVERSITY, ATLANTA, GEORGIA

Why do humans blush? We're the only primate that does so in response to embarrassing situations (shame), or when caught in a lie (guilt), and one wonders why we needed such an obvious signal to communicate these self-conscious feelings. Blushing interferes with the unscrupulous manipulation of others. Were early humans subjected to selection pressures to keep them honest? What was its survival value?

ELAINE MORGAN

BEFORE HER DEATH IN 2013, A WRITER OF BOOKS ON EVOLUTION, INCLUDING *THE NAKED DARWINIST* AND *THE DESCENT OF WOMAN*

Darwin concluded that every species has been moulded by the habitat and lifestyle of its ancestors. So far, evolutionists have been unable to agree on an explanation of any of the distinctive physiological hallmarks of *Homo sapiens*. A more lenient reappraisal of Alister Hardy's aquatic origins theory might help. ›

ANDY KNOLL

PALAEONTOLOGIST AT HARVARD UNIVERSITY, CAMBRIDGE, MASSACHUSETTS

Darwin explained how populations adapt to their environments, but Earth is a moving target, continually changing in response to both physical and biological forcings. The dynamic interactions between life and environment are imperfectly understood, but they underpin Earth's history and will determine the world our grandchildren inherit. The solution requires that we interject physiology – the interface between organism and environment – into analyses of how environmental change will affect life on Earth.

EÖRS SZATHMÁRY

THEORETICAL EVOLUTIONARY BIOLOGIST AT THE EÖTVÖS LORÁND UNIVERSITY, BUDAPEST, HUNGARY

Might evolution by natural selection explain complex thought? We know that a form of selection occurs within our brains as we develop and learn – synaptic connections and pathways that work well are reinforced, whereas weak ones deteriorate. But evolution also requires repeated replication and mutation to generate the variation upon which selection works to give adaptive solutions. At first glance nothing seems to replicate in brain tissue. Any search for neuronal replication will have to take place at a different level – perhaps in the patterns of connections between groups of neurons or in their patterns of activity. The idea is not so far-fetched. We already know that genetic evolution by selection is continuously shaping our immune response. If Darwinian dynamics can give us the flexibility to cope with new diseases, why not also the flexibility to find cognitive solutions to novel problems?

DAVID DILCHER

PALAEOBOTANIST, EMERITUS PROFESSOR AT T HE UNIVERSITY OF INDIANA, BLOOMINGTON

At the time of Darwin, the fossil record of flowering plants did not seem to show signs of evolution, leading him to describe their origin as "an abominable mystery". It has taken a philosophical shift for researchers to rectify this. Where previous generations of palaeobotanists placed fossil plants in the living genus they most closely resembled, today we base our analysis upon careful observation of detailed morphological characteristics. As a consequence, we have an emerging fossil record of flowering plants that includes many extinct taxa and would have delighted Darwin.

CHRIS WILLS

EVOLUTIONARY BIOLOGIST, EMERITUS PROFESSOR AT THE UNIVERSITY OF CALIFORNIA, SAN DIEGO

The biggest gap in evolutionary theory remains the origin of life itself. We now know that life began, probably near volcanically active zones, about 3.8 to 3.5 billion years ago, at a time when there was no free oxygen in the atmosphere. In the laboratory it has been possible to replicate such conditions and produce amino acids, primitive membrane-like structures and some of the building blocks of DNA and RNA. More recently, it has been found that, along with protein enzymes, RNA can catalyse chemical reactions, and it has even been possible to construct RNA molecules that can copy parts of themselves. But the gap between such a collection of molecules and even the most primitive cell remains enormous.

STEVEN PINKER

EVOLUTIONARY PSYCHOLOGIST AT HARVARD UNIVERSITY

How does selection leave its fingerprints on the genome? In particular, how does it work on the non-protein-coding parts, and what kinds of variation does it leave behind: a few common genes with small effects or many rare genes with large effects? This is necessary to understand how we differ from chimps and one another, and why we inherit diseases.

KENNETH MILLER

MOLECULAR BIOLOGIST AT BROWN UNIVERSITY, PROVIDENCE, RHODE ISLAND

I don't think there are basic "gaps" in the theory of evolution, which has proven to be a remarkably flexible scientific framework, brilliantly accommodating new data and even new fields of science, like molecular genetics. However, the most profound unsolved problem in biology is the origin of life itself. We know a great deal about the creative chemistry of the early Earth, but not yet enough to solve this problem.

HELENA CRONIN

DARWINIAN PHILOSOPHER AT THE LONDON SCHOOL OF ECONOMICS

Ask not what gaps should be filled in evolutionary theory, but what gaps evolutionary theory should fill. For it is the key to understanding all living things – not least ourselves. It provides the only scientific understanding of human nature, so it should be transforming the social sciences and thereby social affairs, policy-making and our view of our place in the world.

STUART KAUFFMAN

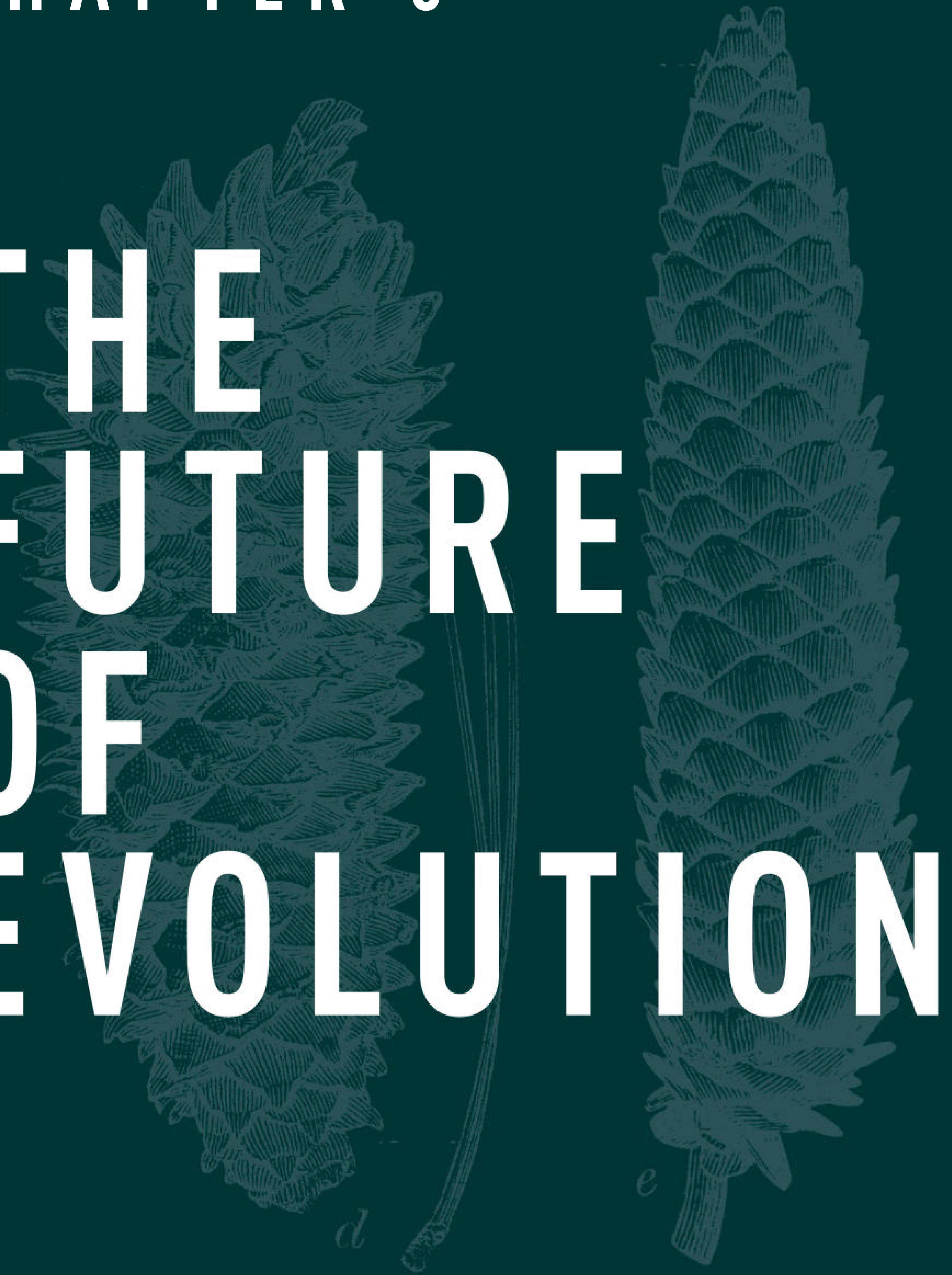
MEDICAL DOCTOR AND THEORETICAL BIOLOGIST, EMERITUS PROFESSOR AT THE UNIVERSITY OF CALGARY, ALBERTA, CANADA

Darwin changed our thinking as much as any scientist. Life, as zoologist Ernst Mayr said, only makes sense in terms of evolution. But major issues arise, such as the fact that Darwin did not know about self-organisation. Abundant work over the past four decades has begun to show that self-organisation plays a role along with natural selection in the order in biology. One example is that lipids spontaneously form liposomes, the hollow bilayered vesicles that must have yielded the cell membrane. Another is the spontaneous order in genetic regulatory networks, the understanding of which may lead to regenerative medicine and new cancer therapies.

SIMON CONWAY MORRIS

PALAEONTOLOGIST AND EVOLUTIONARY BIOLOGIST AT THE UNIVERSITY OF CAMBRIDGE, UK

"Evolution's biggest gap? Quite simple, old boy." Professor Mortimer leaned back and grinned. "Evolution equals change? Naturally, but that is only step one. What is life? A spectacular tightrope walk on a gossamer thread between vast regions of crystalline immobility and chaotic flux. If you don't like that metaphor, try thinking of a pack of cards a mile high with an elephant perfectly balanced on the top. And then there is its uncanny self-organisation. Cells to consciousness – impressive, isn't it? Darwin got it right, and so did Newton. But then physics had Einstein. Perhaps now it is biology's turn."



CHAPTER 6

THE FUTURE OF EVOLUTION

The theory of evolution by natural selection is a gift that keeps on giving – a rich, multi-faceted way of explaining all of the natural world.

But as we've seen, our understanding is a work in progress. For many, the future of evolution means moving beyond the current gene-focused "modern synthesis" to a new, broader view, as Kevin Laland explains

BEYOND THE SELFISH GENE

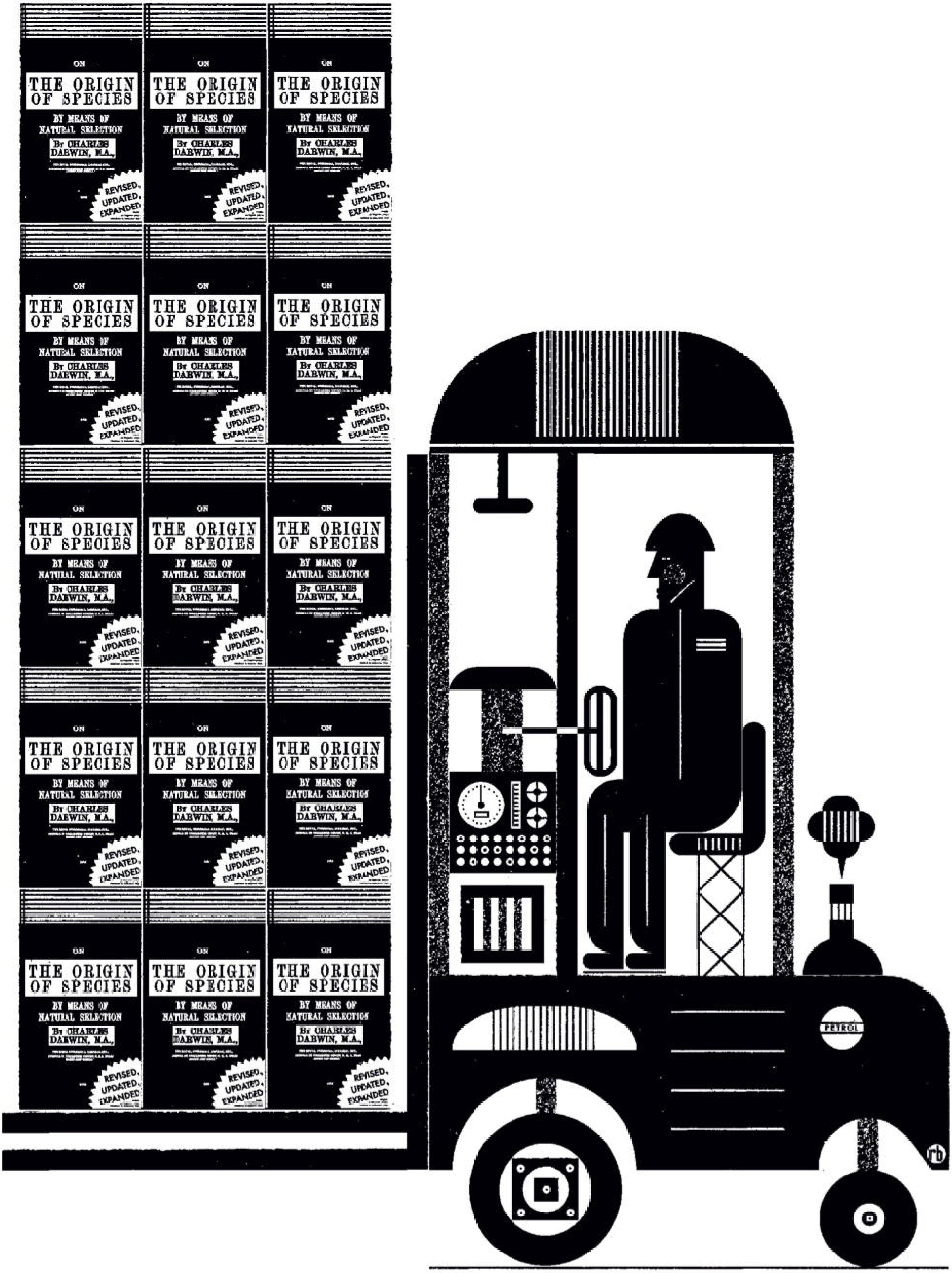
PROFILE
KEVIN LALAND

Kevin Laland is an evolutionary biologist at the University of St Andrews, UK, and the author of books including *Darwin's Unfinished Symphony: How culture made the human mind*

PREVIOUS PAGE: ILBUSCA/ISTOCK
RIGHT: RAYMOND BIESINGER

WHY is life so diverse? And why are living things so exquisitely suited to their environments? To understand these two striking features of the natural world you need look no further than evolution. Darwin's beautiful idea explains why there are hundreds of thousands of species of beetles and flowering plants, why birds' feathers are ideal for flight and insulation, and why a desert plant possesses hairy leaves to reduce water loss. Since *On the Origin of Species* was published in 1859, time has not eroded Darwin's insights.

Yet all scientific theories must incorporate new ideas and findings, and evolution is no exception. In recent years, our understanding of biology has taken huge strides. Advances in genetics, epigenetics and developmental biology challenge us to think anew about the relationship between genes, organisms and the environment, with implications for the origins of diversity and the direction and speed of evolution. In particular, new findings undermine the idea, encapsulated by the "selfish gene" metaphor, that genes are in the driving seat. Instead, they suggest that organisms play active, constructive roles in their own development and that of their descendants, so that ›


ON
THE ORIGIN OF SPECIES
BY MEANS OF NATURAL SELECTION
By CHARLES DARWIN, M.A.,
REVISED, UPDATED, EXPANDED
PETROL
rb

> **“It could be time to let go of the idea that our genes are the blueprint to build our bodies”**

they impose direction on evolution.

Some biologists are trying to shoehorn the new knowledge into traditional evolutionary thinking. Others, myself included, believe a more radical approach may be required. We don’t deny the roles of genetic inheritance and natural selection, but think we should look at evolution in a markedly different way. It is time for the theory of evolution to evolve.

Our current framework for thinking about evolution emerged only in the 1940s, with the integration of new knowledge about evolutionary processes and biological inheritance. This modern synthesis is at the heart of how most people understand evolution. According to this view, the evolution of the features of an organism – collectively known as its phenotype – comes down to random genetic mutation, genetic inheritance and selection of those gene variants that bestow traits best adapted to the environment.

The modern synthesis has served us well: evolutionary biology is developing and thriving. But discoveries made over the past two decades are starting to reveal cracks in some of its central ideas.

Take the notion that heredity happens via genes alone. In a classic 19th-century experiment, German biologist August Weismann cut off the tails of generations of mice, bred from the amputees, and found no reduction in tail length. This led to the view that genetic mutations in the germ line (eggs and sperm) are the only changes passed on to the next generation. But recent experiments suggest a more complex picture.

We now know that things other than genes are transmitted from parents to offspring. These include components of the egg, hormones, symbionts (microorganisms that live inside bodies), epigenetic marks (compounds that bind to DNA and turn genes on and off), antibodies, ecological resources and learned knowledge. At least some of these can lead to stable inheritance of phenotypes. For example, the transmission of epigenetic marks across generations is extremely widespread and, in plants, it can account for differences in fruit size, flowering time and many other traits.

← There’s more on epigenetics on page 77

Epigenetic changes are often induced by changes in conditions within cells or the external environment, such as temperature, stress or diet, and unlike random mutations are often adaptive. Likewise, many animals inherit knowledge from their parents. Cultural inheritance occurs in hundreds of species, not just humans or vertebrates, but invertebrates such as bees and crickets too, creating similarities between even unrelated individuals.

These and many other findings suggest that the current focus on genetic mutations only captures part of the story of adaptive evolution – the slowly changing part. The broader view shows there are other ways to generate heritable variety. It also undermines the clean separation of development and heredity that Weismann’s theory promoted. It is time to let go of the idea that the genes we inherit are a blueprint to build our bodies. Genetic information is only one factor influencing how an individual turns out.

And that’s not all. We now also know that a given set of genes has the potential to produce a variety of phenotypes, depending on the environment in which the organism develops. This ability, called

FPWING/ISTOCK

In bee colonies, cultural inheritance creates similarities between even unrelated individuals

developmental plasticity, used to be dismissed as “noise” or mere “fine-tuning”, but recent research suggests it may play a far more active role in the evolutionary process.

As well as being able to respond in specific ways to particular conditions, organisms seem to have evolved the ability to respond flexibly to whatever conditions they experience. This adaptability results from a sort of Darwinian evolution occurring within organisms. It’s as if each organism evolves as it develops, by generating new variation and selecting what works. This allows systems such as the immune system, nervous system and behavioural systems (through learning) to adjust to meet whatever environment the individual faces.

A flexible phenotype allows organisms to survive in the short term, and may then initiate evolutionary episodes – with genetic change following later. Consistent with this idea, several experiments reveal that organisms exposed to new environments develop characteristics that resemble those of closely related species adapted to these same environments.

For instance, marine sticklebacks reared on diets that are either benthic (bottom-feeding) or limnetic (mid-water) grow to resemble populations adapted to life in the corresponding environment. This suggests that adaptations may commonly arise through immediate responses to the environment, with natural selection favouring such individuals and subsequently cementing the useful features through genetic evolution.

There is also experimental evidence in insects, fish and amphibians that environmentally induced forms can evolve reproductive isolation, meaning that after a while they can no longer interbreed with other

›

members of their species – a key step towards speciation. So developmental plasticity may play a critical role in both adaptation and speciation.

Features of development also undermine orthodox ideas about what factors influence the direction of evolution. The modern synthesis places natural selection in control, regarding it as the sole explanation for adaptation. Evolutionary biologists have tended to think that evolution is not biased in any particular direction, since genetic mutation is assumed to occur at random. However, this idea is challenged by "developmental bias" – the fact that certain characteristics can develop more easily than others. This raises the intriguing possibility that the diversity of life may not only reflect the survival of the fittest but also the arrival of the frequent-est.

Developmental bias could help explain some fascinating quirks of evolution. Consider parallel radiation, in which a species in one location diversifies into several distinct forms and, independently, the same diversification occurs in a different location. A famous example is cichlid fishes living in lakes Malawi and Tanganyika in Africa. Here many species exhibit striking similarities in body shape with different species from the other lake, despite being more closely related to species from their own lake. These body shapes are adaptive, so natural selection has certainly been at play. But the forms we see are not necessarily the only possible adaptive solutions. This suggests there are features of cichlid development that make certain forms particularly likely to arise. Developmental bias could also help explain why cichlids – and some other groups of organisms – are so diverse. It is perhaps because they are particularly good at producing novel variants that can exploit ecological opportunities.

This creative role for development contrasts with its traditional role of imposing constraints on adaptation. Constraints explain the absence of evolution or adaptation, so have been of limited interest. Many evolutionary biologists are now questioning whether this is the best way to think. Perhaps, rather than merely setting limits on what forms are available for selection, developmental bias directs evolution by generating the tramlines along which the engine of selection can proceed.

There is a further way in which organisms might direct their own evolution. Selection is portrayed as a process in which external agents, such as environmental conditions, sort between alternative variants according to their suitability. This is too passive. Organisms are not merely buffeted around by the forces of nature; through their habitat choices and the way they modify their environment, they play active roles in determining which of their characteristics are useful. So they create some of the conditions of their existence, and this influences their evolution.

By building a nest, which reduces temperature fluctuations, for example, a bird weakens selection on the need for physiological regulation of egg temperature, but creates selection for refinements in nest design. Likewise, selection shapes a mammal that digs a burrow less for ways to counter predation, and more for resistance to fungal diseases. Such niche construction is not random, but systematic and directional. The animal manipulates the environment in a consistent, reliable way, to suit itself. In doing so, it biases the action of natural selection, imposing a direction on its own evolution, in much the same way that an animal breeder selects for particular traits in livestock.

Taken together, these discoveries challenge some of the fundamental assumptions of the modern synthesis (see "Modern vs postmodern", right). This new approach gives organisms a central role in their ›

MODERN VS POSTMODERN

Orthodox ideas about how evolution works are being challenged by new discoveries in genetics, epigenetics and developmental biology. This has led some researchers to propose that the current framework, known as the modern synthesis, be broadened into an extended evolutionary synthesis. The fundamentals remain the same, but they rest on quite different assumptions.

MODERN SYNTHESIS	EXTENDED EVOLUTIONARY SYNTHESIS
The major directing influence in evolution is natural selection. It alone explains why the properties of organisms are adapted to match those of their environments.	Natural selection is not solely in charge. The way that an organism develops can influence the direction and rate of its own evolution and its fit to its environment.
Genes are the only widespread system of inheritance. Acquired characters – non-genetic traits that develop during an organism's lifetime – are not inherited and play no role in evolution.	Inheritance extends beyond genes to include epigenetic, ecological, behavioural and cultural inheritance. Acquired characters can be passed to offspring and play diverse roles in evolution.
Genetic variation is random. Mutations that occur are not necessarily fitness-enhancing. It is mere chance if mutations give rise to features that improve the ability of organisms to survive and thrive.	Phenotypic variation is non-random. Individuals develop in response to local conditions, so any novel features they possess are often well suited to their environment.
Evolution typically occurs through multiple small steps, leading to gradual change. That's because it rests on incremental changes brought about by random mutations.	Evolution can be rapid. Developmental processes allow individuals to respond to environmental challenges, or to mutations, with coordinated changes in suites of traits.
The perspective is gene-centred: evolution requires changes in gene frequencies through natural selection, mutation, migration and random losses of gene variants.	The view is organism-centred, with broader conceptions of evolutionary processes. Individuals adjust to their environment as they develop, and modify selection pressures.
Micro-evolutionary processes explain macro-evolutionary patterns. The forces that shape individuals and populations also explain major evolutionary changes at the species level and above.	Additional phenomena explain macro-evolutionary changes by increasing evolvability – the ability to generate adaptive diversity. They include developmental plasticity and niche construction.

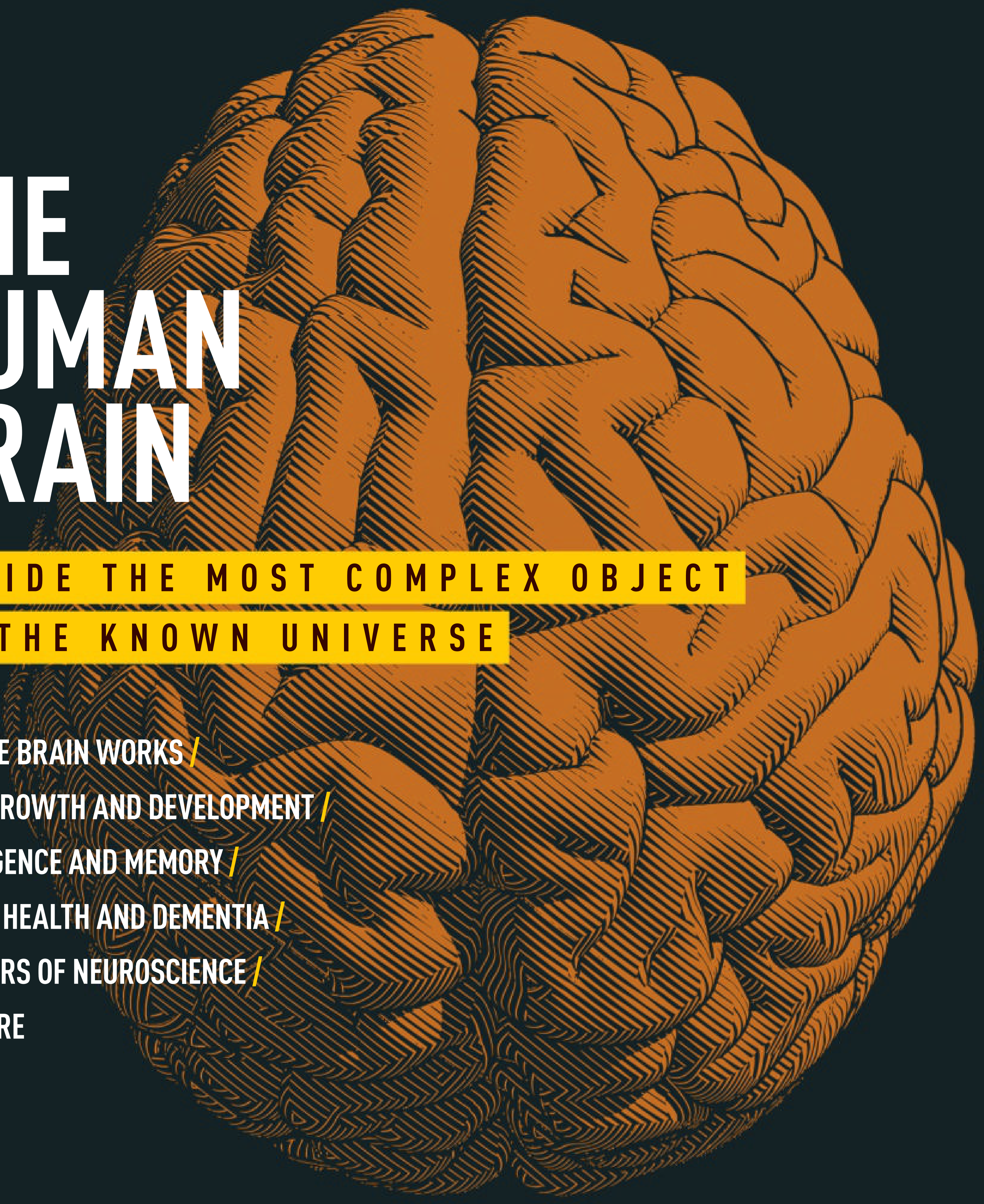
RAYMOND BIESINGER

own evolution, and suggests that novel variation frequently begins not with mutation, but with changes in phenotypes. It indicates that the direction of evolution does not depend on selection alone.

There are two ways to view these new findings: we can try to incorporate them into the old framework, or we can extend the framework. Most evolutionary biologists take the first course, viewing plasticity and niche construction as being under genetic control, and seeing non-genetic inheritance as rare, unstable or functionally equivalent to genes. This view allows genes and selection to retain their explanatory prominence, at the price of downplaying new evidence. The alternative approach is to accept that the modern synthesis struggles to account for the new findings and to propose a broader alternative – an extended evolutionary synthesis. The two types of explanation can then be compared for their predictive power and ability to explain evidence, as well as their productivity in spawning new research questions and methods.

These are exciting times for evolutionary biology, as the full ramifications of these new ideas are explored rigorously for the first time. It remains to be seen whether our efforts will change the orthodox view. What is certain is that over the coming years, these advances will increasingly become the focus for evolutionary biologists.

My own view is that a new conceptualisation of evolution is emerging. The selfish gene has proved to be a powerful and instructive metaphor, but the evidence now suggests it is misleading. Far from being master molecules, genes turn out to be just one of many channels through which cells respond to environmental inputs, and just one of several sources of heredity. Organisms are not the "throwaway survival machines" envisaged by Richard Dawkins and others, but instead often take the lead in their own evolution, dragging genetic change along in their wake. Move over selfish gene, and make way for the orchestrating organism. ∎



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